



Spider behaviours increase trap efficacy

Wonbin Lim¹ · Changku Kang^{1,2,3}

Received: 20 February 2022 / Revised: 26 May 2022 / Accepted: 31 May 2022
© The Author(s), under exclusive licence to Springer-Verlag GmbH Germany, part of Springer Nature 2022

Abstract

Orb-weaving spiders often use their legs to briefly jerk the radii of the web, generating intense vibrations throughout the web. Several functions have been proposed for this behaviour, but there is a lack of empirical evidence. In this study, we conducted a series of experiments on *Cyclosa argenteoalba* to examine the function and adaptive significance of spider jerks in the context of interactions with prey. First, we used within-individual, inter-individual, and interspecific comparisons (in three co-occurring *Cyclosa* sp.) to test whether the relation between prey and spider size predict the frequency of jerks that the spider performs. Second, we examined whether jerks prevent prey from escaping the web, whether jerks entangled more spiral threads around the prey, and how prey size affected this result. We found that spiders jerked more as the prey size increased and as spider size decreased. Jerking behaviour reduced the probability of prey escaping from the web and increased the number of spiral threads contacting the prey. The jerk efficiency (the number of additional spiral threads contacted per jerk) was lower in larger prey, which potentially explains why spiders jerk more towards larger prey. Collectively, our results highlight size dependency in the performance of jerks and their role in prey capture.

Significance statements

Many orb-weaving spiders show a behaviour that pulls the radii of the web intensively using their legs towards their prey, called jerks. Though this behaviour is common and has been recognised for many decades, the function and their adaptive significance have been surprisingly understudied. Using a series of experiments, we demonstrate that jerks help spiders prevent prey escape and subdue prey by entangling additional spiral (sticky) threads around the prey. We further show that the performance of jerks is size-dependent: spiders jerk more (1) as their size decreases and (2) as prey size increases. Further in-depth analysis suggests that the observed size-dependent jerks seem to be related to spiders' cautiousness and/or reduced jerk efficiency towards larger prey.

Keywords Jerk · Predator–prey · Predation · Vibration · Foraging · Adaptation

Communicated by E. M. Jakob

✉ Changku Kang
changkukang@snu.ac.kr

- ¹ Department of Biosciences, Mokpo National University, Jeollanam-do, Cheonggye, Muan 58554, South Korea
- ² Department of Agricultural Biotechnology, Seoul National University, Seoul 08826, South Korea
- ³ Research Institute of Agriculture and Life Sciences, Seoul National University, Seoul 08826, South Korea

Introduction

Trap-building behaviour is one of the most extraordinary prey capture strategies of predators that have captured biologists' attention for a long time (Curio 1976; Dawkins 1982; Lucas 1985; Scharf et al. 2011; Riechert and Łuczak 2014). Generally speaking, the trap increases prey capture efficiency and helps the predator decrease the energy spent during searching for prey (Eltz 1997; Riechert and Łuczak 2014). While traps themselves are often sufficient to capture prey, many trap-building predators have morphological and behavioural adaptations that increase the prey capture efficiency of their traps. For example, larval antlions throw sand to prey to bring it down to the centre of the sandy pits

they dug (Büsse et al. 2021). Likewise, many orb-weaving spiders have bright body colouration or decorations that help lure other insects (Oxford and Gillespie 1998; Cheng et al. 2010; Peng et al. 2020). While predatory traps are taxonomically uncommon (Hansell 2005; Ruxton and Hansell 2009), there is a group of animals that can be easily found in most of the world and are well-recognised for their trap-building behaviour: spiders (Scharf et al. 2011; Riechert and Łuczak 2014; Eberhard 2020).

The spider orb webs capture flying insects in midflight and have at least three functions: interception, stopping, and retention of prey (Eberhard 1990, 2020; Sensenig et al. 2012). Like many other trap-building predators, spiders actively interact with the webs to increase prey capture efficiency (Olive 1980; Herberstein 2011). For example, while waiting for prey, some spiders adjust the tension of the web radii to increase prey detection sensitivity (Watanabe 2000; Nakata 2010) or focus their attention on specific directions of the web that have a higher probability of prey capture (Nakata 2013). Some spiders can discriminate prey types and abandon unprofitable prey (Uetz and Hartsock 1987; Pasquet and Leborgne 1990; Zschokke et al. 2006) or pull the prey closer by rolling up the threads (a behaviour called reeling) (Penna-Gonçalves et al. 2008; Knight 2019; Rao et al. 2019). One of the spiders' prey capture behaviour that is widespread but has received little attention is jerks.

Jerks (also called plucks) describe spiders' behaviour that pulls the radii towards its body using the legs, thereby generating vibrant fluctuations on the web. Jerks are used under various situations, including during courtship (Tarsitano and Kirchner 2001), intraspecific communication (Witt and Rovner 2014), web construction (Eberhard 1973), and prey capture (Robinson and Olazarri 1971; Lubin 1980). Especially, predatory use of jerks can be described in the following way. Once prey is caught on the web, the spider orients itself towards the prey, then shakes the radii vigorously before making direct contact. There have been several hypotheses put forward on the function of jerks. McCook (1889) first suggested that jerking is a means of determining whether objects caught in the web are alive. Robinson and Olazarri (1971) further speculated that jerks help spiders locate prey. For example, some spiders almost always approach the prey immediately when the prey is making struggling vibrations. However, when prey show little or no movement, spiders jerk which induces struggling in motionless prey, enabling the spider to locate the prey (Robinson and Mirick 1971; Lubin 1980). These spider behaviours suggest that jerks may function to locate prey that are caught on the web.

Another function of jerks is preventing prey from escaping and subduing it. The interception of prey on the web does not always mean that it is a ready-to-eat meal. For instance, some prey species escape from the web using standardised

behavioural sequences for escaping (Nentwig 1982; Masters and Eisner 1990). Jerks might disrupt the escape behaviours and decrease its chance by shaking the web vigorously and entangling more spiral threads. In addition, or alternatively, jerks may help spiders avoid potential threats by dangerous prey. Predatory species can pose a severe risk to spiders, even when caught on the web (Olive 1980; Tsai and Pekár 2019); thus, behavioural strategies that suppress the prey's movements reduce such risks. Jerks may be used in this context because the swaying of webs would adhere more spiral threads around the prey, reducing the chance of potentially dangerous movement of prey. However, this prey-subduing hypothesis has never been formally tested.

In this study, we conducted a series of experiments to tackle key unanswered questions regarding the function and adaptive significance of jerks using *Cyclosa argenteoalba* (Araneae: Araneidae) as a model system. First, we tested whether jerks prevent prey from escaping by comparing prey escape chances between spider-present and spider-absent webs. Second, we examined whether spiders perform more jerks towards potentially more threatening prey. Given that larger prey generally pose a greater threat than smaller prey (Mukherjee and Heithaus 2013), we predicted that spiders perform more jerks towards larger prey than smaller ones. We conducted within-, inter-individual, and interspecific (using three co-occurring *Cyclosa* sp.) comparisons to identify whether prey and spider size affect their decision regarding how many jerks they perform before making direct contact. We analysed the spiders' behaviours in various ways, including comparing the approaching time (time from when spiders started responding to prey capture) and jerk efficiency (the number of additional spiral threads that became entangled per jerk) to explain variations in spider behaviours towards differently sized prey.

Methods

No ethics approval was required for research on invertebrates. We adhered to the guidelines for the treatment of animals in behavioural research (Buchanan et al. 2012).

Prey capture behaviour and general experimental procedure

We studied *C. argenteoalba* females to test our hypotheses. *C. argenteoalba* is a small (5–7 mm long) diurnal orb-weaver that is distributed in East Asia and adjacent Russia. When prey is caught on the web, *C. argenteoalba* jerks en route to the prey at various locations (video S1). The captured prey is either brought to the hub or left in the captured area.

In all experiments, we first located mature females along a walking path and gently put a live insect on the web. We

used various insects as prey depending on the hypothesis we tested (see below). Once we located a spider, we held each prey with tweezers and carefully hung it near the left or right outermost spiral threads of the prey capture area to give best chance of observing the jerk behaviour. Prior testings suggested that the distance between the hub and prey affects the number of jerks performed by spiders (Fig. S1). However, controlling for the absolute distance from the hub to prey was practically impossible because the size of the webs differed substantially among spiders. We acknowledge that our way of putting prey on the web differs from how prey will be intercepted in nature. However, this procedure has been successfully adopted in previous studies (Watanabe 2000; Díaz-Fleischer 2005; Rao et al. 2019) and also has the advantage that the experimenter could control factors not under test that can potentially affect spider behaviour such as prey location in the web, variation in the impact of intercepted prey due to the differences in flying speed/direction. Once the prey was hung, we recorded spider behaviours through either direct observations or video recordings (EOS 550D, Canon, Japan). We finished the recording when either the spider captured the prey or the prey escaped from the web. All experiments were conducted under a natural field condition at Mt. Seungdal (Muan-gun, Jeollanam-do, South Korea, 34° 54' 49" N 126° 26' 55" E), 0700–1800 from June to August 2020.

Effect of prey size on jerks

In this experiment, we tested whether prey size affects the number of jerks performed by spiders. We used both within- and inter-individual comparisons. For the within-individual comparison, we provided each spider with three differently sized natural prey collected from our study sites (most were dipteran classified as either small, medium or large size). To classify each prey into one of the three size classes, we first collected insect prey in our study sites, measured each prey's length with a ruler (from the tip of the head to the end of the abdomen) with an accuracy of 0.5 mm, and classified each prey into either small, medium, or large size based on the length. The exact prey size provided for each spider varied, but there was at least a 1-mm length difference among the three prey insects given to each spider. Most of the prey were dipteran (72% of all prey), but there also existed other taxa (especially for larger prey) as well. The three prey (with different sizes) were provided to each spider on the same day. We tested each size class in random order and maintained at least 30-min intervals among each trial. We gently hung the prey on the web for each trial and recorded the number of jerks performed before the spider captured it. It was uncertain whether the spider consumed each prey or not because we left the spider after watching it handling the prey, but the

spiders attacked and jerked every time we provided the prey. We tested 30 individuals.

We used the same approach for the inter-individual comparison (with different individuals) but used only one prey (all dipteran) for each spider. The prey size varied from 2.5 to 6.5 mm. We tested 123 spider–prey pairs and video-recorded spider–prey interactions. Among them, we were able to measure the jerk frequency in 116 videos. The rest seven videos were slightly out of focus, which restricted the accuracy of the jerk frequency measurements. The recorded videos were used again for other analyses as well (see below).

In inter-individual experiments, we used various species of dipterans (we were able to identify most prey species in suborder level, and all of the prey were either in Brachycera or Nematocera) that may behave differently when caught in a web. Because this unstandardisation of prey species (thus prey behaviour) could affect jerk behaviours (Suter 1978; Blackledge and Zevenbergen 2006), we further examined whether there were differences in prey behaviour among different prey size classes by directly analysing prey movement in the videos (see Supplementary materials for the details of analyses). We also checked whether there were behavioural differences between the two suborders of dipteran prey and tested whether the suborder type affected jerk frequencies in spiders (Supplementary materials).

Effect of spider size on jerks

To test whether the spider size affects the number of jerks performed, we used intra- and interspecific comparisons. For intraspecific comparisons, we first provided three different types of prey for each spider (the same individuals used for the within-individual comparison): a pinhead cricket (*Gryllus bimaculatus*; mean length = 2.7 mm, standard deviation = 0.24), a worker termite (*Reticulitermes speratus*; mean length = 3.9 mm, standard deviation = 0.27), and a soldier termite (*R. speratus*; mean length = 5.38 mm, standard deviation = 0.13). We provided prey to each spider in random order, and there were at least 30-min intervals among each trial. We recorded how many times the spiders jerked before direct contact with the prey. We then collected and measured the length (from cephalothorax to abdomen) of the spiders with an accuracy of 0.1 mm by photographic method using ImageJ 1.53e (Schneider et al. 2012).

For interspecific comparisons, we used females of three species of *Cyclosa* genus: *C. sedeculata* (the smallest; 4–5 mm length), *C. argenteoalba* (medium size; 5–7 mm), and *C. octotuberculata* (the largest; 12–15 mm). These three species co-occurred in our field site and differed considerably in size. We conducted this interspecific comparison to examine whether the size dependency in jerks observed within *C. argenteoalba* can be extended to explain the

among-species variation in jerks. We provided the same-sized dipteran prey to all three species (length ≈ 5.5 mm) using the same method described above. We measured and compared the number of jerks performed among the three species. In total, 8, 22, and 12 individuals of *C. sedeculata*, *C. argenteoalba*, and *C. octotuberculata* were used.

Do spider jerks prevent prey from escaping?

To examine whether spider jerks prevent prey escape, we compared the prey escape chance between spider-present (thus performing jerks) and spider-absent conditions. First, to estimate the prey escape chance under the spider-present condition, we used all recorded videos ($N = 123$) of spider–prey interactions. We extracted information on whether each prey successfully escaped from the web before being caught by spiders. We also estimated the mean latency from the moment the prey was caught on the web until prey capture (T_{cap} ; 24 s; standard deviation = 14.27). To investigate the prey escape chance under the spider-absent condition, we located *C. argenteoalba* in the field first (different individuals from the 123 spiders), detached them from the web by lightly touching the spider with a finger (which elicits the response of dropping to the ground), and hung a dipteran prey on the web. Then, we allowed each prey T_{cap} to escape from the web. Rarely the dropped spiders returned to the web before expending T_{cap} , in which case we discarded the trial and moved to the next spider. We tested 29 prey for spider-absent conditions and recorded the prey behaviour. The prey size ranged from 2.5 to 6.5 mm for both treatments. The prey size was controlled when analysing prey escape chance between spider-present and spider-absent conditions (see the ‘Statistical analysis’ section). All spiders jerked towards prey in both prey-escaped and prey-caught situations except for only one individual which successfully caught the prey without jerking.

Do jerks entangle additional spiral threads around prey?

Here, we examined whether jerks add a significant amount of additional spiral threads around prey. We extracted information from the recorded videos of spider–prey interactions (all dipteran prey) to determine the number of additional spiral threads that became entangled with each jerk movement. The spiral threads were additionally entangled around the prey in two different movements: prey struggling and spider jerks. We distinguished these two movements and separately noted whether an additional entangling of spiral threads was caused by prey struggling or spider jerks. We retrieved this information from 49 recordings: in other recordings, the prey was not in focus at some level so that we could not observe

and count the additional number of spiral threads entangled clearly.

Additionally, because spider presence can affect the degree of prey struggling, we also measured the number of additional spiral threads that became entangled by prey struggling under spider-absent conditions. We extracted this information from the 21 recorded videos of spider-absent treatments mentioned above. For each video, we measured (1) the number of additional spiral threads that became entangled by prey movement until T_{cap} and (2) the number of additional spiral threads that became entangled by jerks. We also estimated the jerk efficiency (defined as the number of additional spiral threads that became entangled per jerk) and analysed it.

Comparisons of response and approaching time

In most cases, the spiders responded to the hung prey quickly (88% of all tested spiders responded in 5 s). Still, we measured and analysed the response time (time taken from the prey introduction until the spider responded). Also, the interval between the response initiation and prey capture (approaching time) varied substantially. This interval putatively reflects the level of cautiousness of spiders towards prey. While the absolute distance from the spider and prey may affect spiders’ approaching time, we did not measure and control the distance due to the high variation in web size. However, we consider that the variation in prey-spider distance would contribute to the random variation in spider jerks but not affect spider behaviour in a biased way. We examined whether the approaching time depended on the prey size by analysing the 119 recorded spider–prey interactions.

Statistical analysis

We used R 4.0.2. for all analyses (R Core Team 2018). For the within-individual comparison experiment testing the effect of prey size on the number of spider jerks, we fitted linear mixed models to account for the repeated measurements within individuals implemented in the ‘lme4’ package (Bates et al. 2015). We included prey size as a continuous predictor, spider identification (ID) as a random factor, the number of jerks performed as a response variable. We also used testing order as a covariate in the within-individual comparison analysis. The number of jerks performed was square-root transformed, henceforth to meet the assumptions of the parametric tests. After the transformation, the residuals of the fitted model followed the normal distribution. For the inter-individual comparisons, we fitted a linear regression using the prey size as a predictor and the number of jerks performed as a response variable.

For the intraspecific comparisons testing the effect of spider size on jerks, we employed linear mixed models with spider size, prey type (pinhead, worker, and soldier termites from the smallest to largest), and their interaction as a response variable. We set spider ID as a random factor. We used the number of jerks performed as a response variable. We visually detected one outlier and excluded the individual from the analysis. For post hoc multiple comparisons, we performed Tukey all-pairwise comparisons implemented in the ‘multcomp’ package (Hothorn et al. 2008). Whenever multiple comparisons were used, we controlled for false discovery rates (Benjamini and Hochberg 1995). Also, when multiple response variables were included in a statistical model, we compared the model fit of all candidate models (with all combinations of fixed-effect terms) based on small-sample corrected Akaike information criterion (AICc) and presented the results of the model with the lowest AICc. For the interspecific comparisons, we fitted general linear models (GLMs) using species as a predictor and the number of jerks performed as a response variable to test whether the number of jerks differed among the three *Cyclosa* species. Tukey all-pairwise comparisons were performed as a post hoc test.

We fitted generalised linear models (GLZs) with a binomial error structure to analyse whether jerks decreased the prey’s escape chance. We put a binary variable whether a prey successfully escaped or not as a response variable. For predictors, we first included the presence/absence of spiders (a binary variable). Because prey size could affect the escape probability (Nentwig 1982; Nakata 2010), we also used the prey size and the interaction between prey size and spider presence as additional predictors.

When analysing whether jerks helped entangle prey with additional spiral threads, there existed three measurements for comparison: the number of additional spiral threads entangled (1) by prey movement under the spider-absent condition (PS –), (2) by prey movement under the spider-present condition (PS +), and (3) by spider jerks (JS +). To

compare these, we employed the Kruskal–Wallis rank-sum test with the above group as a predictor and the number of additional spiral threads entangled around the prey as a response variable. For post hoc comparisons, we used the approximative Wilcoxon–Mann–Whitney test employed in the ‘coin’ package (Hothorn et al. 2006). This test estimates *P*-values based on Monte Carlo simulations and deals with tie values well.

To test whether the prey size predicts (1) the number of spiral threads additionally entangled by jerks and (2) the jerk efficiency (the number of additional spiral threads that became entangled per jerk), we fitted linear regressions for each response variable separately.

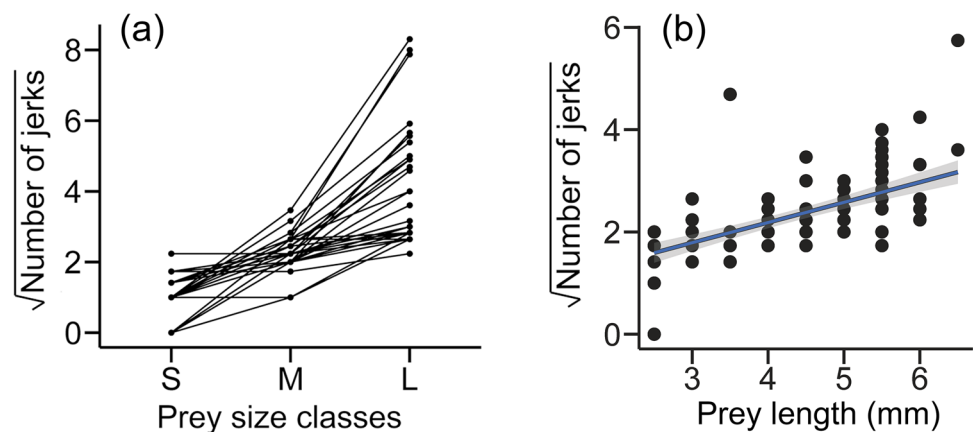
For the response time analysis, we fitted GLMs using the log-transformed response time as a response variable and the prey size as a predictor. We employed a similar GLM to analyse approaching time using log-transformed approaching time as a response variable and prey size as a predictor. Naturally, if a spider is going to perform more jerks, they inevitably spend more time approaching the prey. Thus, we set the number of jerks performed as a covariate to examine whether spiders spent more time approaching larger prey even after controlling for the more frequent jerks made toward them.

Results

Does the frequency of jerks depend on prey size?

The number of jerks increased with prey size in both within-individual (Fig. 1a; estimate = 0.65, s.e. = 0.04, $\chi^2_1 = 232.55$, $P < 0.001$; see Fig. S2 for the plot using prey size as a continuous variable) and inter-individual (Fig. 1b; estimate = 0.39, s.e. = 0.05, $F_{1,114} = 75.95$, $P < 0.001$) comparisons. We found no evidence that testing order affected the number of jerks in within-individual comparisons ($\chi^2_1 = 1.92$, $P = 0.17$). We further elucidated whether there were differences in prey

Fig. 1 The relationship between prey size and number of jerks towards the prey in **a** within-individual ($N = 30$ spiders) and **b** inter-individual comparison experiments ($N = 116$). The line in **(b)** shows the predicted values from linear regression, and the shadowed area shows 95% confidence intervals



movement among differently sized prey which could potentially affect spider jerks (see Supplementary materials for the details about prey movement categories). In inter-individual experiment, we found no evidence that the movement types of prey in the web differed among differently sized prey (Fig. S3; $\chi^2 = 11.74$, simulated $P = 0.15$). While the prey movement types differed between two suborders of the prey we used (Fig. S4a; $\chi^2 = 39.00$, simulated $P = 0.0005$), we found no evidence that prey suborder affected the spider jerks (Fig. S4b; see Supplementary materials for statistics). Also, the observed relationship between prey size and spider jerks were robust regardless of the type of prey movement in the web (Fig. S5).

Does the frequency of jerks depend on spider size?

In intraspecific comparisons, the best model retained spider size and prey type terms, but not the interaction between the two (AIC weight of the best model = 0.53). In the best model, the number of jerks decreased with spider size after controlling for the prey type (Fig. 2a; estimate = -0.30 , s.e. = 0.13 , $\chi^2_2 = 5.79$, $P = 0.02$). We also found strong evidence that prey type affected the number of jerks performed ($\chi^2_2 = 40.21$, $P < 0.001$). Post hoc comparisons confirmed that spiders performed more jerks towards larger prey, then subsequently performed fewer jerks as the prey size decreased (Fig. 2a, P_{adj} for each pairwise comparison was < 0.01).

Interspecific comparisons revealed that the number of jerks towards prey (similar-sized dipteran sp.) differed among spider species (Fig. 2b; $\chi^2_2 = 66.56$, $P < 0.001$). The smallest species, *C. sedeculata*, jerked significantly more than both *C. argenteoalba* (mid-sized species; $Z = 5.58$, $P_{\text{adj}} < 0.001$) and *C. octotuberculata* (largest species; $Z = 8.16$, $P_{\text{adj}} < 0.001$). *C. argenteoalba* also jerked more than *C. octotuberculata* ($Z = 3.98$, $P_{\text{adj}} < 0.001$).

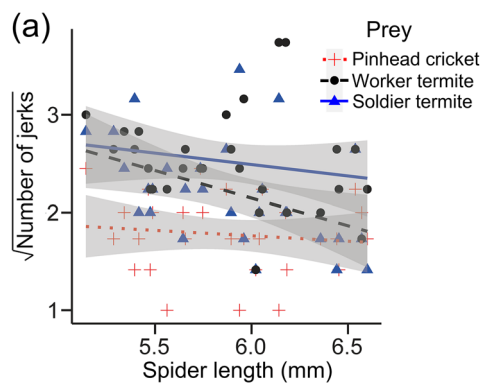


Fig. 2 The relationship between spider size and the number of jerks in **a** intraspecific ($N = 29$) and **b** interspecific comparison experiments. In **(a)**, three different prey (from the smallest pinhead crickets to the largest worker termite) were used. Lines show the predicted values from linear regressions for each prey type. Shaded areas

Do jerks prevent prey escape?

The best model retained spider presence and prey size terms, but not the interaction between the two (AIC weight = 0.51). In the best model, the probability of prey escaping from the web was lower when spiders were present (Fig. 3; $\chi^2_1 = 8.09$, $P = 0.004$). Of the prey, 21% (6 out of 29) successfully escaped from the spider web when spiders were absent, while only 4% (5 out of 123) escaped when spiders were present until T_{cap} (24 s). The escape chance increased as the prey size increased ($\chi^2_1 = 3.74$, $P = 0.05$).

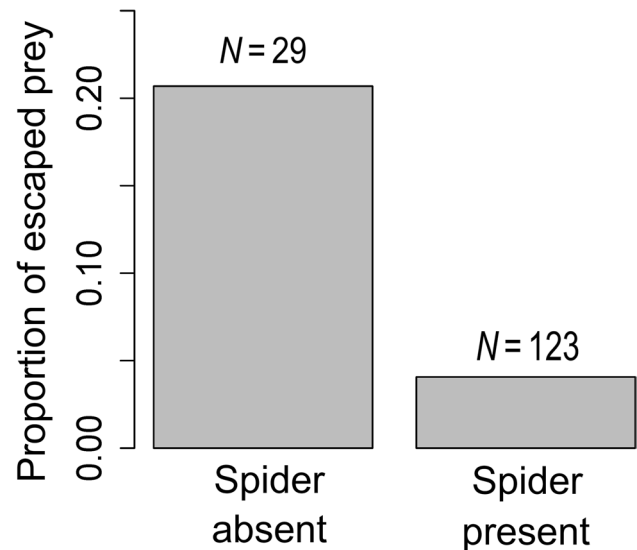
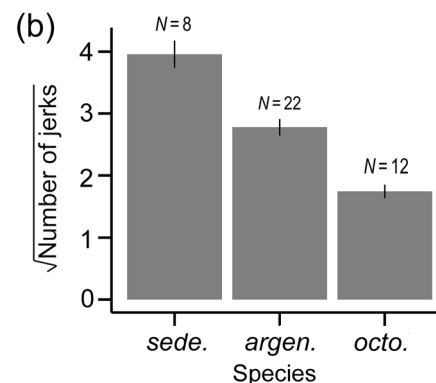


Fig. 3 The results of the prey escape experiment showed the difference in the proportion of successfully escaped prey under spider-present and absent conditions



show 95% confidence intervals. In **(b)**, similar-sized dipteran prey were given to three different co-occurring species of the *Cyclosa* genus. sede: *C. sedeculata* (the smallest), argen: *C. argenteoalba* (medium), octo: *C. octotuberculata* (the largest). Bars and error bars show the mean and standard error of the mean, respectively

Do jerks entangle prey with additional spiral threads?

We found strong evidence that the number of additional spiral threads entangled around the prey differed among the three groups (Fig. 4a; Kruskal–Wallis $\chi^2_2 = 67.25$, $P < 0.001$). Post hoc tests revealed that the number of additional threads entangled was significantly more in JS + groups (spider-present condition) than both the PS + (entangled by prey struggle in spider-present condition) ($Z = 7.49$, $P_{adj} < 0.001$) and PS – (entangled by prey struggle in spider-absent condition) groups ($Z = 5.49$, $P_{adj} < 0.001$). We found no differences between the PS + and PS – groups ($Z = 0.44$, $P_{adj} = 0.69$). On average, 3.80 spiral threads were entangled solely by spider jerks, while only 0.57 and 0.48 spiral threads were additionally entangled by prey movements under spider-absent and spider-present conditions, respectively.

Prey size did not predict the number of additional spiral threads entangled by jerks (estimate = 0.08, s.e. = 0.11, $F_{1,47} = 0.53$, $P = 0.47$). However, the jerk efficiency (the number of additional spiral threads that became entangled per jerk) decreased as the prey size increased (Fig. 4b; estimate = -0.20, s.e. = 0.04, $F_{1,46} = 31.43$, $P < 0.001$). We detected one outlier and removed this from the jerk efficiency analysis, but the inference did not differ whether we removed the outlier or not.

Do the response and approaching times depend on prey size?

We found no evidence that prey size predicts the response time of spiders (estimate = 0.12, s.e. = 0.07, $\chi^2_1 = 2.62$, $P = 0.11$). However, spiders spent more time approaching

prey prior to capture as the size of the prey increased (Fig. 5; estimate = 0.1, s.e. = 0.05, $\chi^2_1 = 4.38$, $P = 0.03$). The covariate effect (number of jerks performed) was also significant (estimate = 0.13, s.e. = 0.01, $t = 94.17$, $P < 0.001$).

Discussion

Our results indicate two inter-related functions of jerks: preventing prey from escaping and entangling more spiral threads around the prey. The prey escape chance

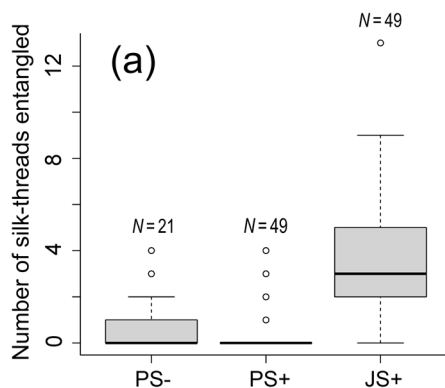


Fig. 4 a Comparison of the additional number of spiral threads entangled around the prey (1) due to prey struggling under spider-absent condition (PS –), (2) due to prey struggling under spider-present condition (PS +), (3) due to spider jerks (JS +). Each boxplot shows the median, first, and third quartiles. Dots show outliers. **b** Relationship

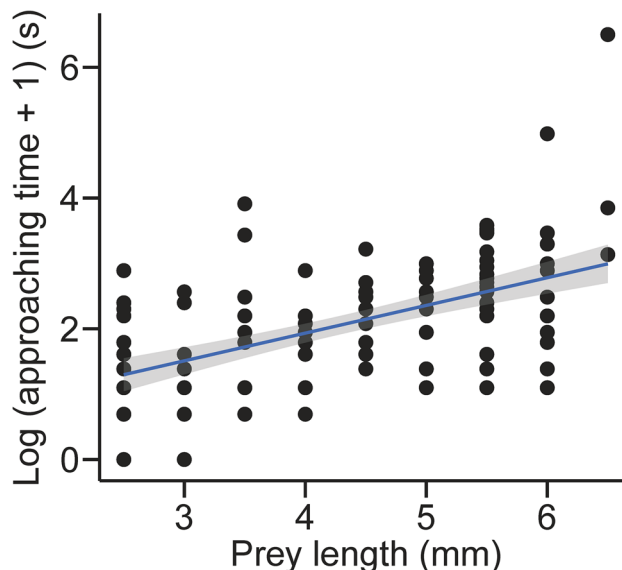
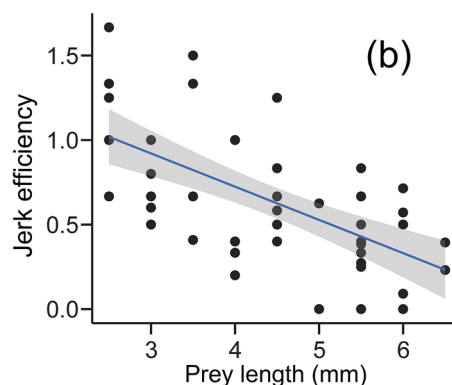


Fig. 5 The relationship between prey size and approaching time (defined as the time from the spider responding to prey and prey capture) ($N = 119$). Lines show the predicted values from linear regression, and the shadowed area shows 95% confidence intervals



between prey size and jerk efficiency (the number of additional spiral threads that became entangled around the prey per jerk) ($N = 48$; one outlier removed). The line shows the predicted values from linear regression, and the shadowed area shows 95% confidence intervals

substantially decreased when the spiders were present and performed jerks than spider-absent conditions. This may have been largely induced by the additional spiral threads entangled around the prey due to the jerks. Prey movement itself did not contribute much to the additional spiral threads entangled around the prey. Besides the additionally entangled spiral threads, spider jerks may also have prevented prey from adopting specialised behavioural sequences required to escape from the web (Suter 1978; Masters and Eisner 1990). Some prey insects perform specific behaviours, such as cutting away sticky strands, wriggling, or turning, which help them escape (Nentwig 1982). Web fluctuations caused by jerks would disrupt prey to adopt such stances. Indeed, we observed that some dipteran prey showed certain behaviours, such as wiping the wings with their legs and rubbing the legs, to remove the attached spiral threads (video S2). This occasionally led to a successful escape in a short time (in our study, 21% of the tested dipteran prey escaped within 24 s). However, under the presence of spider jerks, only a few prey (4% of the total) could escape within the same time. We note here that the prey escape experiment did not follow proper randomisation procedures (such as interspersing testing webs with and without spiders or randomising testing orders) that minimise the effect of confounding factors. However, considering (1) the large difference in prey escape chance between the treatments and (2) that there is no reason to consider that web location or testing time (which are the main potential confounding factors affected by non-randomisation) affected our results in a biased way, we argue that the non-randomisation issue will not invalidate our results.

Both within- and inter-individual comparisons testing the prey size effect on jerks revealed that spiders jerk more as prey size increases. Also, both intra- and interspecific comparisons suggest that smaller spiders jerk more than larger spiders. The results of interspecific comparisons need to be cautiously interpreted because the three *Cyclosa* species not only differ in size but also in other traits such as web characteristics (Miyashita 1997). Still, considering that all within-, inter-individual, and interspecific comparisons all consistently follow the predicted size-jerk relationship, body size should be at least partly responsible for the observed behavioural difference among the three *Cyclosa* species. Collectively, all the evidence suggest that both prey size and spider size determine the number of jerks performed towards the prey. These results are congruent with previous findings on size-dependent jerks in other spiders (Díaz-Fleischer 2005; Rao et al. 2019). To answer why spiders jerk more towards larger prey, we propose two alternative but non-exclusive explanations related to the function of jerks.

First, the more frequent jerks that spiders exhibit towards larger prey may be related to their wariness towards larger prey. Like many predators, spiders can subdue and consume prey in various sizes (Nentwig and Wissel 1986; Riechert and Łuczak 2014). In general, larger prey elicit more risk to spiders than smaller prey (Mukherjee and Heithaus 2013). Under this circumstance, spiders are expected to approach large prey cautiously and exhibit more jerks (Rao et al. 2019). This is well reflected in the results we obtained for the approaching time: spiders took more time to approach larger prey than smaller prey. Another point of view is that spiders jerk more towards larger prey because the efficiency of jerks depends on prey size. Although the number of additional spiral threads entangled by jerks was not affected by prey size in our results, the jerk efficiency decreased with the increasing prey size, possibly because larger/heavier objects are more resistant to being swayed given the same amount of power exerted on it. This suggests that spiders (especially smaller spiders) should jerk more towards larger prey to entangle a sufficient number of spiral threads around the prey. This can consequently lead to size-dependent jerks performed by spiders.

In conclusion, we demonstrated that spider jerks have adaptive significance in preventing prey escape and entangling more spiral threads around prey. All the evidence consistently indicate that the performance of jerks is size-dependent. This seems to be related to spiders' cautiousness or reduced jerk efficiency towards larger prey or both. Understanding the behaviour of trap-building predators and how it is shaped by both internal and external factors have been of the recent research interest (Eberhard 2020; Büsse et al. 2021; Scharf et al. 2021; Abot et al. 2022), but empirical evidence of the functions of these behaviours are limited (Eberhard 2020). While jerks have been described in a wide range of spiders for a long time (McCook 1889; Briceño and Eberhard 2011), there has been no direct evidence of their adaptive role and function during foraging. Our results provide firm evidence of the function of spider jerks and highlight the size-dependent use of jerks. While our study on *Cyclosa* sp. focuses on the use of jerks during foraging, spiders also use jerks in other contexts such as during courtship or communications (Bleckmann and Bender 1987; Uetz and Stratton 2014). Further studies on the function of jerks in other contexts should provide a more comprehensive understanding of this widespread and multifaceted behaviour.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00265-022-03189-3>.

Author contributions CK and WB conceived the ideas, designed the experiments; WB collected the data; WB and CK analysed the data; WB drafted the initial version of the manuscript; and all authors contributed to revising the manuscript.

Funding This research was supported by the National Research Foundation of Korea (grant no: NRF-2019R1C1C1002466).

Data availability Data are available as supplementary material.

Declarations

Conflict of interest The authors declare no competing interests.

References

- Abot AR, Arguelho EG, do Nascimento Lima T (2022) Foraging behavior plasticity in antlion larvae *Myrmeleon brasiliensis* (Neuroptera, Myrmeleontidae). *Int J Trop Insect Sci* 42:591–595
- Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. *J Stat Softw* 67:1–48. <https://doi.org/10.18637/jss.v067.i01>
- Benjamini Y, Hochberg Y (1995) Controlling the false discovery rate: a practical and powerful approach to multiple testing. *J R Stat Soc B Stat Methodol* 57:289–300. <https://doi.org/10.1111/j.2517-6161.1995.tb02031.x>
- Blackledge TA, Zevenbergen JM (2006) Mesh width influences prey retention in spider orb webs. *Ethol* 112:1194–1201. <https://doi.org/10.1111/j.1439-0310.2006.01277.x>
- Bleckmann H, Bender M (1987) Water surface waves generated by the male pisaurid spider *Dolomedes triton* (Walckenaer) during courtship behavior. *J Arachnol* 363–369
- Briçeño RD, Eberhard WG (2011) The hub as a launching platform: rapid movements of the spider *Leucauge mariana* (Araneae: Tetragnathidae) as it turns to attack prey. *The J Arachnol* 39:102–112. <https://doi.org/10.1636/Hi10-76.1>
- Buchanan K, Burt de Perera T, Carere C et al (2012) Guidelines for the treatment of animals in behavioural research and teaching. *Anim Behav* 83:301–309. <https://doi.org/10.1016/j.anbehav.2011.10.031>
- Büsse S, Büscher TH, Heepe L, Gorb SN, Stutz HH (2021) Sand-throwing behaviour in pit-building antlion larvae: insights from finite-element modelling. *J R Soc Interface* 18:20210539
- Cheng RC, Yang EC, Lin CP, Herberstein ME, Tso IM (2010) Insect form vision as one potential shaping force of spider web decoration design. *J Exp Biol* 213:759–768. <https://doi.org/10.1242/jeb.037291>
- Curio E (2012) The ethology of predation. Springer Science & Business Media. [https://doi.org/10.1016/0376-6357\(77\)90022-5](https://doi.org/10.1016/0376-6357(77)90022-5)
- Dawkins R (1982) The extended phenotype. Oxford University Press, UK
- Díaz-Fleischer F (2005) Predatory behaviour and prey-capture decision-making by the web-weaving spider *Micrathena sagittata*. *Can J Zool* 83:268–273. <https://doi.org/10.1139/z04-176>
- Eberhard WG (1990) Function and phylogeny of spider webs. *Annu Rev Ecol Syst* 21:341–372
- Eberhard WG (1973) Stabilimenta on the webs of *Uloborus diversus* (Araneae: Uloboridae) and other spiders. *J Zool* 171:367–384. <https://doi.org/10.1111/j.1469-7998.1973.tb05345.x>
- Eberhard W (2020) Spider webs: behavior, function, and evolution. University of Chicago Press, Chicago. <https://doi.org/10.7208/chicago/9780226534749.001.0001>
- Eltz T (1997) Foraging in the ant-lion *Myrmeleon mobilis* hagen 1888 (neuroptera: Myrmeleontidae): Behavioral flexibility of a sit-and-wait predator. *J Insect Behav* 10:1–11
- Hansell MH (2005) Animal architecture. Oxford University Press, UK. <https://doi.org/10.1093/acprof:oso/9780198507529.001.0001>
- Herberstein ME (2011) Spider behaviour: flexibility and versatility. Cambridge University Press, Cambridge. <https://doi.org/10.1017/CBO9780511974496.004>
- Hothorn T, Bretz F, Westfall P (2008) Simultaneous inference in general parametric models. *Biom J* 50:346–363. <https://doi.org/10.1002/bimj.200810425>
- Hothorn T, Hornik K, Van De Wiel MA, Zeileis A (2006) A lego system for conditional inference. *Am Stat* 60:257–263. <https://doi.org/10.1198/000313006X118430>
- Knight K (2019) How arrowhead spiders reel in tasty prey. *J Exp Biol*. <https://doi.org/10.1242/jeb.218990>
- Lubin YD (1980) The predatory behavior of Cyrtophora (Araneae: Araneidae). *J Arachnol* 8:159–185
- Lucas JR (1985) Metabolic rates and pit-construction costs of two antlion species. *J Anim Ecol* 295–309
- Masters WM, Eisner T (1990) The escape strategy of green lacewings from orb webs. *J Insect Behav* 3:143–157. <https://doi.org/10.1007/BF01417908>
- McCook HC (1889) American spiders and their spinning work: snares and nests (Vol 1). Academy of Natural Sciences of Philadelphia, Philadelphia. <https://doi.org/10.5962/bhl.title.66025>
- Miyashita T (1997) Factors affecting the difference in foraging success in three co-existing *Cyclosa* Spiders. *J Zool* 242:137–149. <https://doi.org/10.1111/j.1469-7998.1997.tb02935.x>
- Mukherjee S, Heithaus MR (2013) Dangerous prey and daring predators: a review. *Biol Rev* 88:550–563. <https://doi.org/10.1111/brv.12014>
- Nakata K (2010) Attention focusing in a sit-and-wait forager: a spider controls its prey-detection ability in different web sectors by adjusting thread tension. *Proc R Soc B Biol Sci* 277:29–33. <https://doi.org/10.1098/rspb.2009.1583>
- Nakata K (2013) Spatial learning affects thread tension control in orb-web spiders. *Biol Lett* 9:20130052. <https://doi.org/10.1098/rsbl.2013.0052>
- Nentwig W (1982) Why do only certain insects escape from a spider's web? *Oecologia* 53:412–417. <https://doi.org/10.1007/BF00389023>
- Nentwig W, Wissel C (1986) A comparison of prey lengths among spiders. *Oecologia* 68:595–600. <https://doi.org/10.1007/BF00378777>
- Olive CW (1980) Foraging Specialization in Orb-Weaving Spiders. *Ecol* 61:1133–1144. <https://doi.org/10.2307/1936833>
- Oxford GS, Gillespie RG (1998) Evolution and ecology of spider coloration. *Annu Rev Entomol* 43:619–643. <https://doi.org/10.1146/annurev.ento.43.1.619>
- Pasquet A, Leborgne R (1990) Prey capture efficiency and prey selection from insects intercepted by trap in four orb-weaving spider species. *Acta Oecol* 11:513–523
- Peng P, Stuart-Fox D, Chen SW, Tan EJ, Kuo GL, Blamires SJ, Tso IM, Elgar MA (2020) High contrast yellow mosaic patterns are prey attractants for orb-weaving spiders. *Funct Ecol* 34:853–864. <https://doi.org/10.1111/1365-2435.13532>
- Penna-Gonçalves V, Garcia CRM, Japyassú HF (2008) Homology in a context dependent predatory behavior in spiders (Araneae). *J Arachnol* 36:352–359. <https://doi.org/10.1636/CS07-118.1>
- R Core Team (2018) R: a language and environment for statistical computing
- Rao D, Tapia-McClung H, Narendra A (2019) Reeling in the prey: fishing behaviour in an orb web spider. *J Exp Biol* 222:jeb213751. <https://doi.org/10.1242/jeb.213751>
- Riechert SE, Łuczak J (2014) Spider foraging: behavioral responses to prey. In: Spider communication. Princeton University Press, Princeton, pp 353–386. <https://doi.org/10.1515/9781400857517>
- Robinson MH, Mirick H (1971) The predatory behavior of the golden-web spider *Nephila clavipes* (Araneae: Araneidae). *Psyche* 78:57182. <https://doi.org/10.1155/1971/57182>

- Robinson MH, Olazarri J (1971) Units of behavior and complex sequences in the predatory behavior of *Argiope argentata* (Fabricius): (Araneae: Araneidae). *Smith Contrib Zool* 65:1–36
- Ruxton GD, Hansell MH (2009) Why are pitfall traps so rare in the natural world? *Evol Ecol* 23:181–186. <https://doi.org/10.1007/S10682-007-9218-0>
- Scharf I, Gilad T, Taichman Y, Subach A (2021) Urban pit-building insects are attracted to walls for multiple reasons. *Biology* 10:635. <https://doi.org/10.3390/biology10070635>
- Scharf I, Lubin Y, Ovadia O (2011) Foraging decisions and behavioural flexibility in trap-building predators: A review. *Biol Rev* 86:626–639. <https://doi.org/10.1111/j.1469-185X.2010.00163.x>
- Schneider CA, Rasband WS, Eliceiri KW (2012) NIH Image to ImageJ: 25 years of image analysis. *Nat Methods* 9:671–675
- Sensenig AT, Lorentz KA, Kelly SP, Blackledge TA (2012) Spider orb webs rely on radial threads to absorb prey kinetic energy. *J R Soc Interface* 9:1880–1891. <https://doi.org/10.1098/rsif.2011.0851>
- Suter RB (1978) *Cyclosa turbinata* (Araneae, Araneidae): prey discrimination via web-borne vibrations. *Behav Ecol Sociobiol* 3:283–296. <https://doi.org/10.1007/BF00296314>
- Tarsitano M, Kirchner WH (2001) Vibrational courtship signals of *Zygiella x-notata* (Clerck) (Araneae: Araneidae). *Bull Br Arachnol Soc* 12:26–31
- Tsai Y-Y, Pekár S (2019) Prey acceptance and conditional foraging behavior in the cribellate-web spider *Titanoeca quadriguttata* (Araneae: Titanoecidae). *J Arachnol* 47:202–208. <https://doi.org/10.1636/JoA-S-18-083>
- Uetz GW, Hartssock SP (1987) Prey selection in an orb-weaving spider: *Micrathena Gracilis* (Araneae: Araneidae). *Psyche* 94:16298. <https://doi.org/10.1155/1987/16298>
- Uetz GW, Stratton GE (2014) Acoustic communication and reproductive isolation in spiders. In: Witt PN, Rovner JS (eds) *Spider communication*. Princeton University Press, Guildford, pp 123–160. <https://doi.org/10.1515/9781400857517>
- Watanabe T (2000) Web tuning of an orb-web spider, *Octonoba sybotides*, regulates prey-catching behaviour. *Proc R Soc B Biol Sci* 267:565–569. <https://doi.org/10.1098/rspb.2000.1038>
- Witt PN, Rovner JS (2014) *Spider communication: mechanisms and ecological significance*. Princeton University Press, Guildford. <https://doi.org/10.1515/9781400857517>
- Zschokke S, Hénaut Y, Benjamin SP, García-Ballinas JA (2006) Prey-capture strategies in sympatric web-building spiders. *Can J Zool* 84:964–973. <https://doi.org/10.1139/z06-074>

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.