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# Computational analyses of dynamic visual displays reveal diet-dependent male signalling in *Rabidosa rabida* wolf spiders

Noori Choi [a, *, 1], Dustin J. Wilgers [b], Eileen A. Hebets [a]

[a] *School of Biological Sciences, University of Nebraska-Lincoln, Lincoln, NE, U.S.A.*
[b] *Department of Natural Sciences, McPherson College, McPherson, KA, U.S.A.*

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Male courtship signals vary widely due to genetic, environmental and ecological influences. This study investigates how diet manipulation affects the dynamic visual components of multimodal courtship displays in male *Rabidosa rabida* wolf spiders. Using a Gaussian Hidden Markov Model (GHMM), we implemented an automated bottom-up approach to identify the hierarchical structure of foreleg movements during courtship. We then integrated unary and binary similarity measures to quantitatively compare these movements. Our results show that the GHMM-derived structural organization of foreleg movements closely aligns with classifications made by human observers. Furthermore, combining unary and binary similarity measures provides a robust framework for quantifying dynamic movements in animal communication. Notably, male foraging history influences both foreleg morphology and movement during courtship displays. This study enhances our understanding of the evolution of complex male courtship signals and offers a standardized framework for future research.

Despite important advances in formalizing hypotheses and approaches to study complex animal communication (Bro-Jørgensen, 2010; Candolin, 2003; Hebets & Papaj, 2005; Partan & Marler, 1999, 2005), our understanding of the form and function of distinct signal components (which may vary within and across individuals and within and across sensory modalities) remains incomplete (Hebets, 2011; Hebets et al., 2016; Higham & Hebets, 2013). The predominant context in which we study complex animal communication is within reproductive interactions, and as such, we know that courtship signals can vary within and across individuals due to genetic (Gleason et al., 2002; Miller & Brooks, 2005), developmental (Lomborg & Toft, 2009; Rosenthal & Hebets, 2012), environmental (Beckers & Schul, 2008; Taylor et al., 2005; Wilgers & Hebets, 2011) and ecological factors (Choi et al., 2022; Yang et al., 2024), among others. We further know that courtship displays may consist of multiple signal components that vary in functions and/or production mechanisms, and the degree to which internal and external factors affect courtship signals may vary across these signal components (Blankers et al., 2017; Bro-Jørgensen, 2010; Larter et al., 2023; Tanner et al., 2017). For instance, the body weight of male Túngara frogs, *Engystomops pustulosus*, influences the amplitude of whines but is not related to any properties of chucks. Male Túngara frogs, however, increase the number of chucks when they court in a denser conspecific chorus (Larter et al., 2023). Thus, whine amplitude may be an indicator of male size, whereas chuck number is influenced by the frog's social environment, suggesting component-specific selection.

Given the variation in how multivariate selection acts differently on different signal components (either in isolation or as a composite), our understanding of how courtship signals evolve will depend on how researchers define, identify and study discrete signal components. To date, many studies have targeted predominantly static, sexually dimorphic, morphologically based visual signalling components and assessed their potential informational content (for content-based hypotheses of complex signal function, see Hebets & Papaj, 2005). Researchers, for example, have identified multiple systems with condition-dependent colour signalling,

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* Corresponding author.
*E-mail address:* noori.choi@uni-konstanz.de (N. Choi).
[1] Present address: Centre for the Advanced Study of Collective Behaviour, University of Konstanz, Konstanz, Germany.

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for example, carotenoid-based plumage brightness of male house finches (Hill, 1990; Hill & Montgomerie, 1994; McGraw & Hill, 2000), colour expression in fish and its link to sperm quality and fertility (Locatello et al., 2006; Pike et al., 2010; Rahman et al., 2013) and carotenoid-based skin coloration and its relationship with individual quality in tree frogs (Benes-Soto et al., 2017; Vásquez & Pfennig, 2007). However, not colour per se, diet-dependent ornamentation (dark pigmentation and brush size) has even been widely documented across numerous wolf spider species (Hebets et al., 2006, 2020; Rosenthal & Hebets, 2015). Unlike predominantly static colour-based visual signals, however, quantifying condition dependence in dynamic visual signals poses several unique challenges.

Dynamic signals or those that change in intensity, pattern or movement over short timescales, play a critical role in animal communication. Motor performance during courtship, for example, is hypothesized to be a major factor in signaller mating success, as it is proposed to reflect whole-organism performance (Byers et al., 2010). Indeed, courtship displays across animal groups require metabolic investment (Dearborn et al., 2005; Mowles & Jepson, 2015; Vehrencamp et al., 1989), suggesting a high cost and thus an indication of signaller quality. However, just as we observe in static complex signals, dynamic signals often involve multiple discrete signal components that can be distinguished by their characteristic movement patterns (Dalziell et al., 2013; Eilam, 2023; Miles & Fuxjager, 2018). Again, as with static complex signals, the distinct components of dynamic displays may serve different functions or may indicate different aspects of signaller quality. Direct tests of an indicator function of signal components often involve manipulations of quality (e.g. through diet manipulations, immune challenges, etc.) and subsequent assessments of signal component form. The challenge, however, is in how to identify discrete signal components from dynamic displays that show continuous temporal variations in multiple features. Furthermore, it is not even clear whether breaking down a dynamic display into discrete components is the most appropriate approach to understanding dynamic signal function.

Nonetheless, ‘experts’ have traditionally created ethograms of complex behaviour, which have provided a comprehensive reference for identifying signal components within particular study systems (Nelson et al., 2022; Odom et al., 2021; Stanger-Hall & Lloyd, 2015; Vedenina & Mugue, 2011). Using this approach, researchers first divided a signal repertoire into smaller segments (often termed ‘signals’ or ‘signal components’) by distinct and identifiable changes such as silent gaps, frequency modulation, amplitude modulation, etc. (Odom et al., 2021). These signal components are then manually clustered and labelled based on structural similarities. Regardless of the quality of ethograms, however, the scale and numbers of the signal components have often been a subject of debate. For instance, there is much uncertainty and discussion around how to define the minimum discrete unit consisting of continuous songs or body movements (Anderson & Perona, 2014; Kohlsdorf et al., 2020; McCullough & Goodhill, 2021; Okafor et al., 2017; Sainburg et al., 2020; Sheppard et al., 2022; Whiteway et al., 2021). Similarly, questions arise regarding how ‘similar’ observed signal components have to be classified into one of the pre-established categories, both within and across individuals and species (Kershenbaum & Garland, 2015; Odom et al., 2021). Decisions are not always agreed upon by other experts, and as such, an ethogram-centred approach is not always reproducible across researchers or studies, raising questions about their validity. Previous studies on Lake Tanganyikan cichlid communication, for example, have primarily relied on manually classified ethograms (Lein & Jordan, 2021). Noted inconsistencies in the established ethograms are, however, common, even within studies of the reference species (*N. pulcher*: 17 behavioural categories in Sopinka et al., 2009 versus 13 categories in Hick et al., 2014).

To overcome the drawbacks of using manually defined ethograms for identifying and quantifying the function(s) of signal components, many researchers have paired experimental manipulations of signaller conditions with quantitative tools to categorize animal displays through a ‘bottom-up’ approach. Such an approach defines (hierarchical) structures of animal sounds or movements from the smallest discrete units in fine temporal scales, usually in a few milliseconds (e.g. eigenshape, Stephens et al., 2008; eigensound, Rocha & Romano, 2021; gesture, Eilam, 2023), to the upper structural levels, which are the stereotyped occurrence patterns (or motifs) of the discrete units identified at the lower structural levels (Arthur et al., 2013; Berman et al., 2014; Kohlsdorf et al., 2014; Stephens et al., 2008). Furthermore, such a process is usually automated using computational techniques, including motion tracking (Berman et al., 2014; Stephens et al., 2008) and audio recognition (Arthur et al., 2013; Kohlsdorf et al., 2014). This automated bottom-up approach allows researchers to annotate organizations of dynamic multicomponent signals in verifiable and updatable ways that can be reproduced by other researchers, making it a potentially powerful tool. Thus far, the development and testing of these toolsets have predominantly focused on only a few animal groups, including nematodes (Stephens et al., 2008), fruit flies (Arthur et al., 2013; Berman et al., 2014) and dolphins (Kohlsdorf et al., 2014). In this study, we aim to expand this to a study exploring dynamic visual signalling in a multimodal signalling wolf spider with dynamic visual displays.

Male *Rabidosa rabida*, Walckenaer, wolf spiders produce multimodal courtship displays (Rovner, 1967, 1968) encompassing substrate-borne vibrations produced by pedipalp stridulations (Rovner, 1967, 1968) and dynamic visual display components involving pedipalp waving and arching/extending of the ornamented forelegs (Kaston, 1936; Rovner, 1968). Like other wolf spider systems (e.g. *Schizocosa*; Herberstein & Hebets, 2013), *R. rabida* has been used as a model system for testing hypotheses about the evolution of complex courtship signals (Wilgers & Hebets, 2011; 2012a; 2012b). Prior research exploring the form and function of *R. rabida* courtship displays showed that (1) diet manipulation influenced both male vibratory signals (Wilgers & Hebets, 2012a) and foreleg ornamentation (Wilgers & Hebets, 2011). These studies demonstrated condition-dependent signalling of both vibratory and static visual (i.e. foreleg ornamentation), suggesting that they function as indicator traits. (2) Female *R. rabida* were shown to prefer to mate with well-fed males (Wilgers & Hebets, 2012b), indicating a preference for ‘quality’ mates. Finally, (3) the static visual display (i.e. leg ornamentation) affected male mating success in the presence of vibratory signals (Wilgers & Hebets, 2012a). This latter finding indicates an interaction between vibratory and visual signalling in which vibratory signalling might focus a female's attention on visual details. A similar effect of vibratory signalling influencing a receiver's visual attention was documented in the wolf spider, *Schizocosa uetzi* (Hebets, 2005). Research on other wolf spiders in the genus *Schizocosa* has also shown interesting interactions between foreleg ornamentation and dynamic visual signalling (*Schizocosa stridulans*, Hebets, 2008; *Schizocosa bilineata*, Hebets et al., 2020). To date, however, although we know that vibratory and static visual signal components of *R. rabidosa* courtship provide females with information on a male's past foraging history, nothing is currently known about the function of dynamic visual courtship signalling.

In this study, we explored the condition dependence of the dynamic visual component (i.e. foreleg movements) of the multimodal courtship displays of *R. rabida* using a ‘bottom-up’ approach to quantifying the intraspecific variations in the dynamic signalling following diet manipulations, high versus low quantity diet. To quantify the resulting variation, we first developed a tool to define the minimum structural unit (i.e. foreleg posture) and the hierarchical structure of foreleg movements during the complex courtship display of *R. rabida* using the Gaussian Hidden Markov Model (GHMM). Then, we used both traditional 'unary' and recently proposed 'binary' (see Methods for full explanations of unary and binary) measures for quantifying the similarities of the identified structural organizations of complex visual displays of male *R. rabida* wolf spiders. Ultimately, our study develops and tests novel methods for quantifying variation in dynamic visual signalling as a means of testing its diet-dependence and potential indicator function in the wolf spider *R. rabida.*

## MATERIALS AND METHODS

### *Study Animals and Diet Manipulation*

Immature *R. rabida* were collected in Lancaster County, Nebraska (40°44′57″ N; 96°49′4″ W) from 3 June 2007 to 12 June 2007. In the laboratory space with a controlled light cycle (15:9 h light:dark) and temperature (21 °C–27 °C), we housed animals in individual plastic cages (60 × 60 × 80 mm). Immediately upon collection, we randomly assigned males to high ($N = 30$) and low diets ($N = 14$) and fed them two body size-matched crickets, *Acheta domestica*, twice a week (high diet) and once every 2 weeks (low diet), respectively. All the females were fed twice a week (high diet). There was no significant difference in the body weight between high- and low-diet males before the diet treatment (Wilcoxon rank-sum test: $W = 243$, $P = 0.82$). We supplemented the crickets given to the spiders with Fluker's cricket feed, Fluker's cricket quencher (Fluker Farms, Port Allen, LA, U.S.A.) and fish food. We checked the spiders for moults (shed exoskeleton) 2–3 times a week to watch for maturation or the final developmental stage when sexual organs are present. The number of days from the final moult varied from 12 to 58 days. These males were used for other experiments to test the effect of diet on mate choice and courtship display. There was no significant effect of the number of days from the final moult and prior experiments (mating success, days from the experiment) on the results of the present experiment (Supplementary Material).

### *Male Courtship Quantification*

To ensure that males were motivated to court, we first placed them in a 'priming arena' intended to elicit male courtship displays (Tietjen, 1979). Our priming arena contained a live female and silk cues from four different females. To prepare the silk cues, we placed four different virgin *R. rabida* females in circular arenas (diameter = 20.2 cm, height = 7.3 cm) and allowed them to lay silk on pieces of round filter paper (Whatman #1, 185 mm) for more than 12 h. We then cut and pieced together quarter sections of each of the four female silk-laden filter papers to line the bottom of the priming arena (the same type of circular plastic arena; diameter = 20.2 cm, height = 7.3 cm). The silk-laden filter papers were replaced after each male's trial. We also placed one of the four females (haphazardly chosen) in the priming arena with the male to incentivize male courtship. One min after a male started courtship signalling, we transferred him to the filming arena (rectangular plastic arena; width: 127 mm, depth: 33 mm and height: 135 mm).

The recording arena was notably smaller than the priming arena so as to restrict the male's locomotory movement and facilitate more controlled spider framing (e.g. angles and depth). The back of the recording arena was covered with graph paper to provide the contrast that aids in display tracking as well as a known size calibration using the grid. To encourage continued courtship in the filming arena, the bottom of the arena had pieces of the same female-silk–laden filter papers as the priming arena. To provide a visual cue for courting males that also helped orient them into a position that enabled us analyse their display, we moved the female from the priming arena to just outside the video recording arena in a plastic vial (diameter = 3.8 cm, height = 8.5 cm). We used one of 13 virgin females as the visual cue for courting males and found no effect of female ID on our results of male courtship clustering (Binomial logistic regression: Wald $\chi^2_{12} = 2.871$; $P = 0.996$).

We recorded male displays using a Sony DCR-HC65 NTSC Handycam (Sony Electronics, San Diego, CA, U.S.A.). The recording was initiated when the courting first began in the filming arena and ended when either the courting finished or more than 10 useable male courts had been observed. All males except one in the high-diet treatment had already been used once in a previous mate choice trial (Wilgers & Hebets, 2012b), but as stated previously, we found no effect of prior experience on our results (Supplementary Material).

We analysed the movement of the male foreleg during the selected courtship bouts using ProAnalyst Lite software (Xcitex, Woburn, MA, U.S.A.). We chose the first courtship bout in which males move their forelegs from the cocked position without any locomotion of the males (Fig. 1a) and tracked the change in the location of the different parts of the foreleg used in courtship (that is, males do not wave both legs during courtship displays). This criterion may have affected the position of the selected bouts within the total courtship sequence, but it did not influence the results of the analysis (Supplementary Material). We tracked six parts of each foreleg, including (1) the insertion of the foreleg, (2) the femur–patella joint, (3) the patella–tibia joint, (4) the

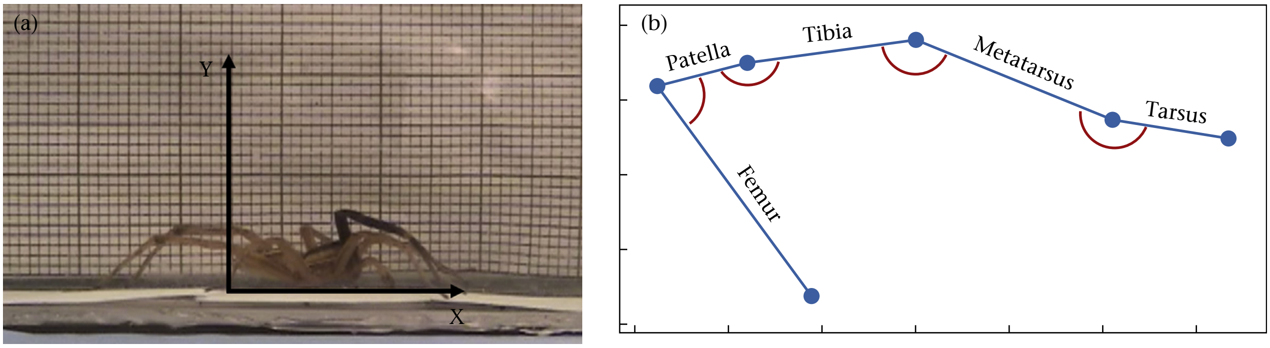

**Figure 1.** Video analysis of visual courtship display. (a) *x* and *y*-axis in ProAnalyst Lite at the 'cocked' position of courting males. (b) Leg segments and the angles between adjacent segments.

tibia–metatarsus joint, (5) metatarsus–tarsus joint and (6) the leg tip (Fig. 1b). Given the short length of leg segments, the coxa, trochanter and femur were regarded as the same segment (femur; Fig. 1b). After video analysis, we calculated the (1) distance between each joint and foreleg insertion, (2) angles between each joint and the *x*-axis and (3) angles between adjacent foreleg segments (Fig. 1b).

## *Structural Organizations of Dynamic Visual Display*

### *Inferring hidden states of foreleg posture*

To define the structural organization of foreleg movements in *R. rabida* males, we used a GHMM to identify discrete units of foreleg movements by inferring hidden states (i.e. foreleg postures). These hidden states consist of multivariate time series data, including (1) angles between each joint and the *x*-axis, (2) angles between adjacent foreleg segments and (3) the first- and second-order derivatives of both variables, which represent the instantaneous velocity and acceleration/deceleration of joint movements, respectively. These features were extracted from all video frames to capture both the spatial configuration and dynamic properties of foreleg motion. The GHMM assumes that variations in these input variables from the video frames are associated with the distribution of hidden states (i.e. foreleg postures) during the visual courtship displays of male *R. rabida*. The temporal transitions among behavioural states are modelled as a first-order Markov chain, meaning the probability of transitioning between states at a video frame *t* depends only on the transition probability matrix at a video frame *t* and the state at the previous video frame *t-1*.

Although the Von Mises distribution is commonly used for circular data, our analysis showed that the angular measurements in our data set were approximately normally distributed due to the nature of foreleg movements. Based on this, we chose a Gaussian distribution for its computational efficiency and compatibility with standard HMM implementations. Additionally, our primary focus was on capturing the overall structure of movement patterns rather than strict angular periodicity, making the Gaussian assumption a practical and effective choice.

To determine the optimal number of hidden states in the GHMM, we used the following three criteria: the Akaike Information Criterion (AIC), the Bayesian Information Criterion (BIC) and the Log-Likelihood (LL), all of which are widely used in similar studies (Heerah et al., 2017). We selected the optimal number of hidden states, ranging from 1 to 14, by identifying the local minimum of AIC and BIC and the local maximum of LL (Fig. S1). To validate the optimal GHMM model, we used a random forest model, a machine learning algorithm that classifies data by aggregating decisions from multiple decision trees. We trained the model using the input variables and the GHMM-predicted behavioural states to assess how well the states could be distinguished based on movement features (Fig. 2). We visualized the clusters of defined foreleg postures in the optimal GHMM model using Uniform Manifold Approximation and Projection (UMAP; McInnes et al., 2018).

We used the hmmlearn (Lefebvre, 2023), scikit-learn (Pedregosa et al., 2011), SciPy (Virtanen et al., 2020) and UMAP (McInnes et al., 2018) Python packages for GHMM modelling and verification. The corresponding code is provided in Dryad repository (Choi et al., 2025).

### *Defining structural organization of foreleg movement*

To define the structural organization of male foreleg movement, we searched the stereotyped occurrence pattern of hidden states (i.e. foreleg postures) using both visual inspections of graphical representations (Figs. 3 and 4) and motif discovery algorithms for bioinformatics, Multiple Expectation maximizations for Motif Elicitation (MEME; Bailey & Elkan, 1994). Once we identified stereotyped occurrence patterns, hereafter referred to as motifs, each consisting of three distinct foreleg postures, we compared them with previous descriptions of signal components in male *R. rabida* visual displays (Rovner, 1968; Fig. 4). We then identified broader phases of foreleg movements, which were distinguished based on the occurrence patterns of motifs, with each phrase consisting of multiple motifs. For MEME, we used the online MEME Suite program (Bailey et al., 2015). The detailed results of MEME can be found in Fig. S2 and Dryad repository (Choi et al., 2025).

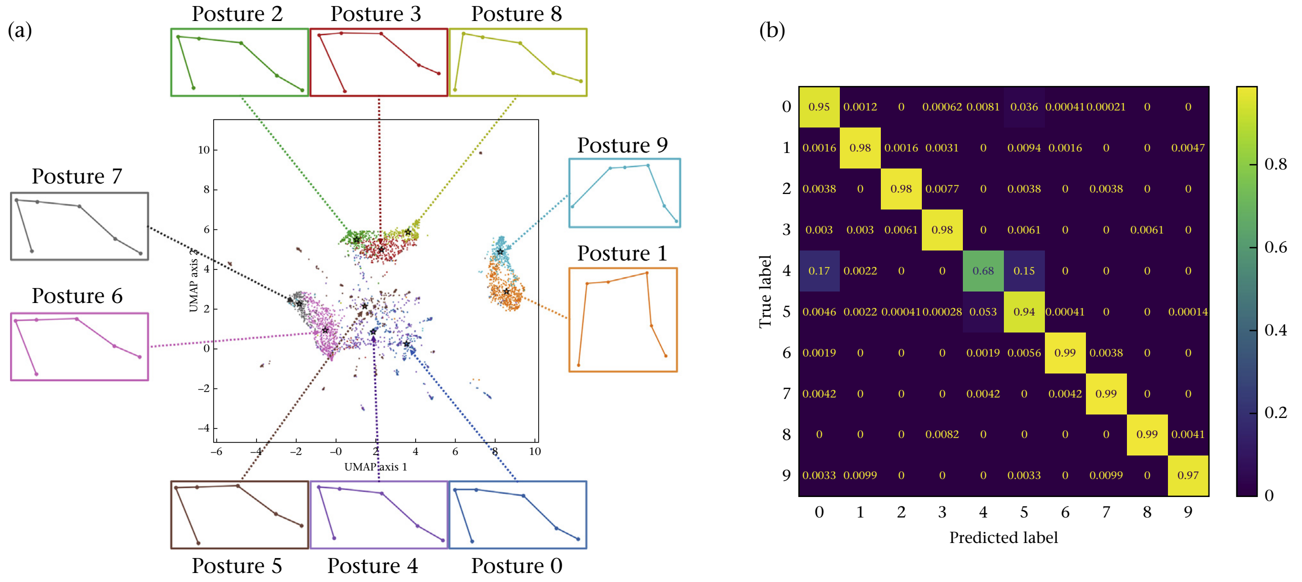

**Figure 2.** The behavioural states (i.e. foreleg posture) identified by the GHMM model. (a) The presentation of the distribution of foreleg postures in the Uniform Manifold Approximation and Projection (UMAP) space (*n_neighbour* = 500). Each dot represents a video frame from recordings of *R. rabida* foreleg movements during courtship display. Labels and representative images are shown around the UMAP plot. (b) The classification accuracy by a random forest model. The 'true label' refers to the labels assigned by the GHMM model, whereas the 'predicted label' refers to those predicted by the random forest model.

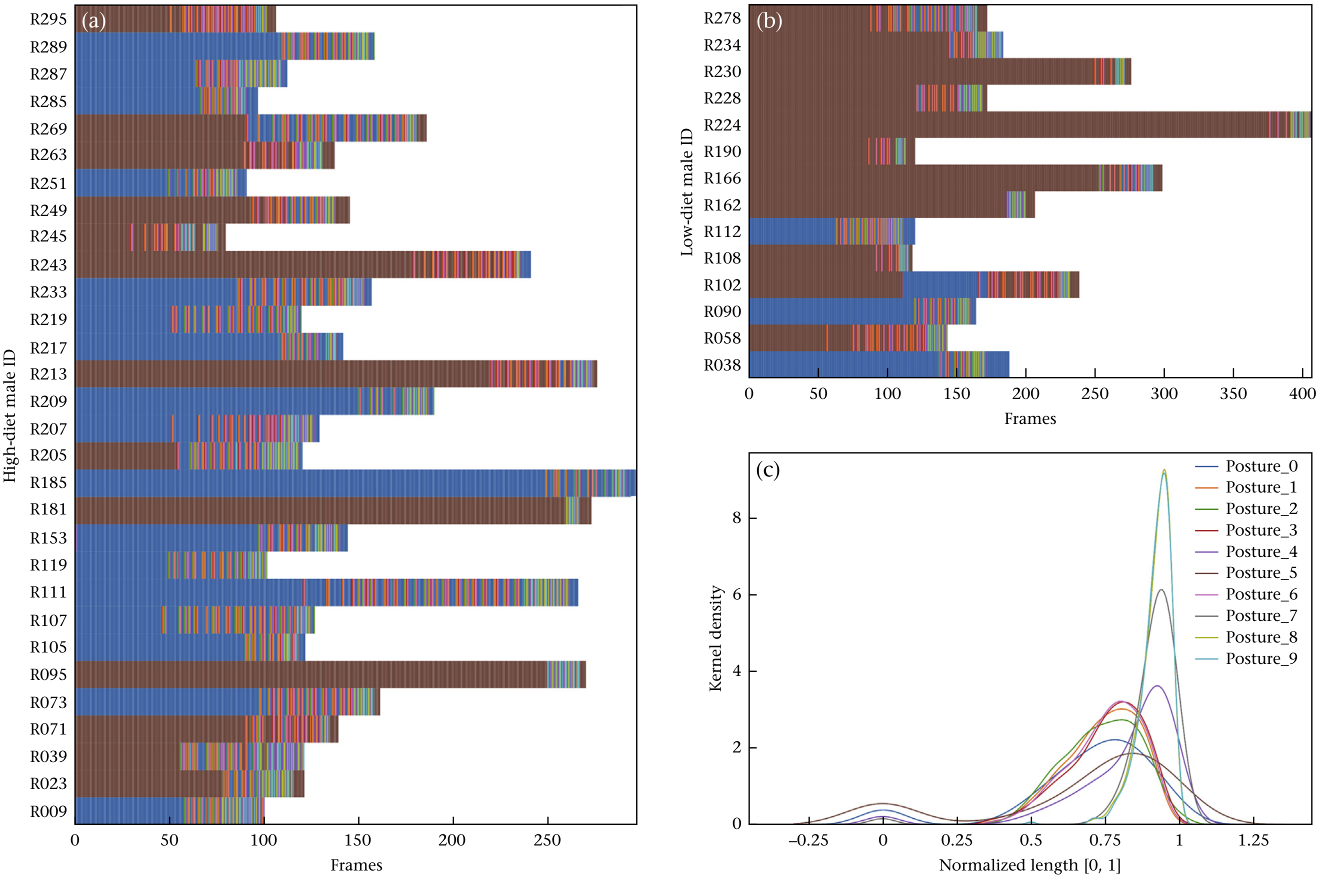

**Figure 3.** The representation of male foreleg movements as a temporal sequence of behavioural states (i.e. foreleg posture). Foreleg movements of (a) high-diet and (b) low-diet males. (c) Kernel density estimation of the occurrence of each behavioural state in the foreleg movements with normalized length from 0 to 1. Colour coding corresponds to the foreleg postures shown in Fig. 2.

### *Diet-Dependence of Dynamic Visual Display*

Before the quantitative comparison of foreleg movements that were annotated by the GHMM model, we investigated the potential impacts of diet manipulation on morphological variation in the length of each foreleg segment using a linear regression model.

#### *Unary similarity measures of foreleg movement*

Unary measures summarize the characteristics of individual signals using various features ranging from duration (Cady et al., 2011) to signal complexity (Choi et al., 2022). The similarity is then estimated using relatively simple metrics such as Euclidean distance in the feature space or numerical differences of each feature. Although unary measures are most used in animal communication studies, finding the optimal set of features to fully represent the variation in complex signals is a challenging task. Additionally, comparing multicomponent signals using unary measures requires identifying discrete signal components, adding another challenging task. Nonetheless, we use unary measures as a comparison to binary measures.

Following the defined structural organization of foreleg movement of *R. rabida* males (that is, stationary, leg-arching and leg-extension phases), as unary measures of the similarity in male foreleg movements, we quantified the (1) duration, (2) numbers and rate of foreleg movements and (3) complexity of temporal sequences of total (that is, display as a whole) and each phase (that is, stationary, leg-arching and leg-extension phases) of male courtship display. To quantify the complexity of temporal sequences, we calculated Lempel–Ziv complexity (Lempel & Ziv, 1976), Shannon entropy (Shannon, 1948) and entropy rate (Cover & Thomas, 1999). Then, we conducted linear and generalized linear regressions to investigate the effects of (1) the male diet, (2) the body weight ratio between a male and visual stimuli female and (3) the interaction terms on the quantified features.

#### *Binary similarity measures of foreleg movement*

Binary measures directly quantify the pairwise differences in signal structures without the need for feature selection. The binary approach is analogous to similarity measures used for various sequence data such as DNA, proteins and text documents (Rieck, 2011). Although binary measures can bypass the feature selection required for unary measures, many binary metrics assume the subjects being compared have comparable units with the same lengths (e.g. alphabets, pixels and nucleotides). To adapt binary measures for quantitative comparison of animal signals, researchers must be able to (1) identify the comparable units (i.e. signal components) and (2) assess the differences among these units. For instance, to quantify binary measures (e.g. Levenshtein distance and dynamic time warping [DTW] distance) to compare male courtship signals A-B-B-A-C, A-C-C-B-A and A-D-C-B-A, researchers should (1) identify the signal components A, B, C and D and (2) define the distance matrix between signal components, considering that the differences are not homogeneous. These prerequisites for binary measures present similar challenges to those faced with unary measures.

To quantify the direct pairwise similarity among foreleg movements of individual males without feature selection, we utilized DTW distance. To compute the DTW distance, we represented the

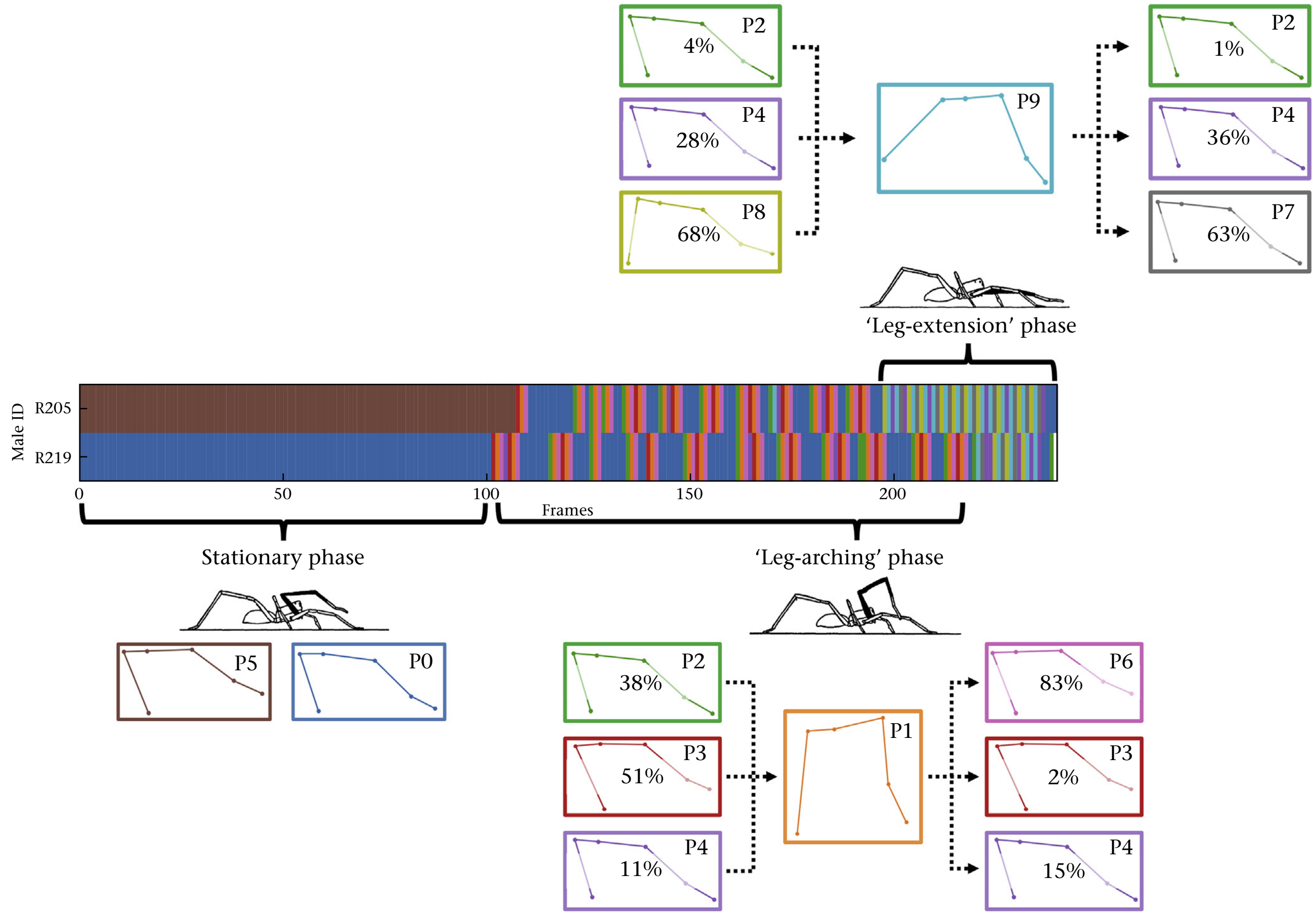

**Figure 4.** The structural organization of foreleg movements of *R. rabida* males. Foreleg movements consist of three major phases: stationary, leg-arching and leg-extension, with a highly conserved temporal order among them. Panels above or below each phase illustration depict the stereotyped occurrence patterns observed within that phase. Values on foreleg posture images indicate the probability of occurrence at that position, whereas the absence of a value represents 100% occurrence. Foreleg posture labels (e.g. P0 and P1) are denoted in the upper right corner of each image. The illustrations of the foreleg movements of *R. rabida* are from Rovner (1968).

structural organization of foreleg movements as a temporal sequence comprising (1) behavioural state (i.e. foreleg posture) and (2) the duration of consecutive occurrences of the foreleg shape (hereafter referred to as segments). We then measured the similarities of foreleg movements as a product of two distinct DTW distances: shape-DTW and length-DTW.

For shape-DTW, the alignment cost between two points is quantified by pairwise weighted Euclidean distances among foreleg postures based on the input variables: (1) angles between each joint and the $x$-axis, (2) angles between adjacent foreleg segments and (3) the first and second derivatives of both variables. Given that the input variables contribute variably to the GHMM model, we quantified the Euclidean distance with weights estimated from the feature importance derived from the random forest model for GHMM model validation. Therefore, the alignment cost between two points for shape-DTW is given by

$$d(a,b) = \sqrt{\sum_{i=1}^{n} (w_i \cdot (a_i - b_i))^2}$$

when $w_i$ is the feature importance of the $i$th input variables (e.g. angles between patella and tibia) of two points from a pair of foreleg movements, $a_i$ and $b_i$. To reduce the computational costs, we assigned the median value of all pairwise weighted Euclidean distances as the alignment costs of the corresponding pairs of foreleg postures.

For length-DTW, the cost of alignment between two points is the differences in the duration of segments normalized by the min–max normalization. The normalized duration $x'$ is calculated as

$$x' = \frac{x - \min(A \cup B)}{\max(A \cup B) - \min(A \cup B)}$$

when A and B are the set of segment durations of a pair of foreleg movements.

Using these binary similarity measures, we investigated whether males subjected to low- and high-diet conditions showed distinct patterns of foreleg movements through agglomerative clustering. We then performed a multinomial logistic regression with (1) the male diet, (2) the body weight ratio between a male and a visual stimulus female and (3) the interaction terms as predictor variables to determine if these factors could predict clustering results of male foreleg movements. We present a visual explanation of the binary similarity measures in Fig. S3.

Additionally, we conducted linear and generalized linear regressions to examine the effects of (1) cluster, (2) the body weight ratio between a male and a visual stimulus female and (3) the interaction terms on the unary similarity measures, which included duration, numbers and rates of foreleg movements and the complexity of temporal sequences in total and each phase of male courtship display. The duration of each phase was normalized as a proportion of the total courtship display time. Through this analysis, we explored the utility of combining unary and binary similarity measures for studies in animal communication.

We conducted the statistical analysis using R version 4.2.2 for Windows (R Core Team, 2023). Assumptions such as normality, homoscedasticity and linearity were checked through visual inspection of residuals versus fitted values and QQ plots. The models showed no violations of key assumptions, and the residuals were randomly distributed around zero.

### *Ethical Note*

No special protocols were required for the handling or use of spiders in research. We nevertheless ensured the proper maintenance and ethical care for all spiders in our study. After experiments, spiders were individually euthanized by freezing and then preserved in 70% ethanol. These spiders were all at the end of their natural life as males typically live less than a few months after sexual maturation. To the best of our knowledge, we followed the suggestions of ASAB/ABS Guidelines for the use of animals in research.

## RESULTS

### *Structural Organizations of Dynamic Visual Display*

The GHMM found 10 distinct foreleg postures consisting of the foreleg movement of *R. rabida* males. The presentation of foreleg postures in UMAP space (McInnes et al., 2018) and the classification accuracy of a random forest model support the reliability of the identification of foreleg postures by the GHMM model (Fig. 2).

The kernel density estimation showed that *R. rabida* males use different foreleg postures as their courtship displays progress (Fig. 3). In particular, the occurrence patterns of ‘Posture 1’ and ‘Posture 9’ divided the dynamic visual display into three phases, including stationary, leg-arching and leg-extension phases, which are coincident with the previous description of leg-extension display (Rovner, 1968; Fig. 4). Also, the motif discovery by MEME supports that Posture 1 and Posture 9 are the major foreleg postures in the structural organization by the common occurrences in the detected motifs that match leg-arching and leg-extension. Detected motifs are presented in .gif format in Dryad repository (Choi et al., 2025).

### *Diet-Dependence of Dynamic Visual Displays*

#### *Foreleg morphology*

There were significant differences between high- and low-diet males in the length of the femur ($F_{1,\ 41} = 4.928$, $P = 0.032$), patella ($F_{1,\ 41} = 4.189$, $P = 0.047$) and metatarsus ($F_{1,\ 41} = 6.046$, $P = 0.018$). There was no significant variation due to the male diet on the length of the tibia ($F_{1,\ 41} = 3.156$, $P = 0.083$) and tarsus ($F_{1,\ 41} = 0.284$, $P = 0.597$). Across the segments that were significantly different, high-diet males had longer foreleg segments compared with low-diet males (Fig. 5).

#### *Unary similarity measures*

Diet treatment significantly influenced (1) the duration of stationary and leg-arching phases, (2) the number of leg-arching postures and (3) the Shannon entropy of total visual courtship display (Table 1). The duration of the bout of courtship display of low-diet males produced longer visual courtship displays (13.364 ± 5.404 s) than high-diet males (10.493 ± 4.197 s). However, low-diet males' courtship displays consisted of a larger proportion of the stationary phase (0.724 ± 0.158) and a smaller proportion of the leg-arching phase (0.174 ± 0.144) than high-diet males (0.614 ± 0.160; 0.271 ± 0.141; respectively; Figs. 6a, 7a and 8a). Due to the smaller proportion of the leg-arching phase, low-diet males produced fewer leg-arching behaviours (11.571 ± 8.373) than high-diet males (15.933 ± 8.366) without a significant variation in the rate of leg-arching behaviours. Also, in total sequences, Shannon entropy was higher in high-diet males' courtship displays (1.464 ± 0.545) than in low-diet males (0.957 ± 0.582).

The weight ratio between female and male *R. rabida* wolf spiders only influenced the number of leg-arching postures. *Rabidosa rabida* males that encountered a heavier female tended to produce more leg-arching behaviours during their visual courtship display

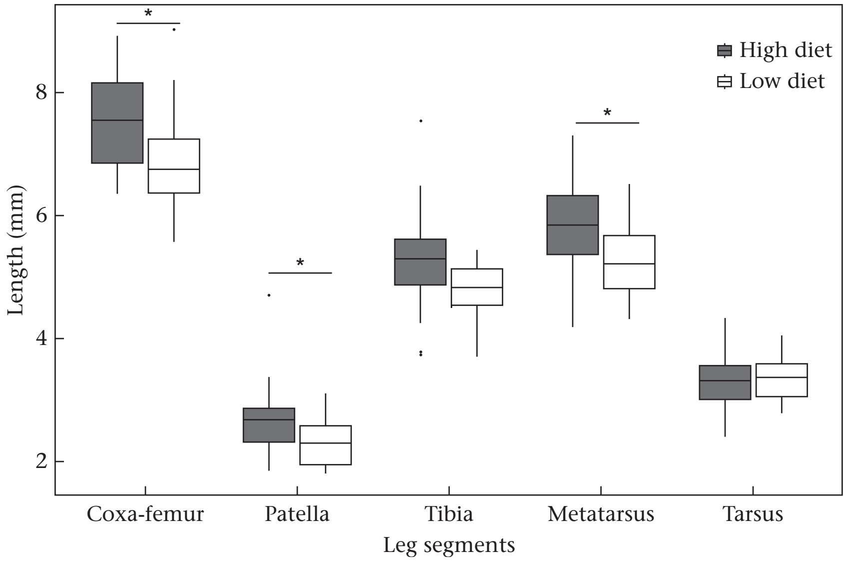

**Figure 5.** The lengths of leg segments of high- and low-diet males. The top, middle and bottom of the box represent the 25th, 50th and 75th percentiles, respectively. The whiskers represent 1.5 times the IQR or most extreme value. Statistically significant differences were denoted by asterisks (*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$).

**Table 1**

The results of regression models of the unary similarity measures with predictors including diet (low versus high diet), weight ratio between female and male spiders and the interaction term

| Dependent variable | Phase | Predictor(s) | *df* | *F* | *P* |
|---|---|---|---|---|---|
| Duration | Total seq. | Diet | 1, 40 | 0.480 | 0.493 |
| | | Weight ratio | 1, 40 | 1.342 | 0.253 |
| | | Diet × weight ratio | 1, 40 | 0.086 | 0.771 |
| | Stationary | Diet | 1, 40 | 6.036 | **0.018** |
| | | Weight ratio | 1, 40 | 1.843 | 0.182 |
| | | Diet × weight ratio | 1, 40 | 0.161 | 0.690 |
| | Leg-arching | Diet | 1, 40 | 7.753 | **0.008** |
| | | Weight ratio | 1, 40 | 3.365 | 0.074 |
| | | Diet × weight ratio | 1, 40 | 0.151 | 0.699 |
| | Leg-extension | Diet | 1, 40 | 3.220 | 0.080 |
| | | Weight ratio | 1, 40 | 3.265 | 0.078 |
| | | Diet × weight ratio | 1, 40 | 5.441 | **0.025** |
| Number of foreleg movements | Leg-arching | Diet | 1, - | 22.913 | **<0.001** |
| | | Weight ratio | 1, - | 20.233 | **<0.001** |
| | | Diet × weight ratio | 1, - | 2.491 | 0.115 |
| | Leg-extension | Diet | 1, - | 0.038 | 0.846 |
| | | Weight ratio | 1, - | 0.662 | 0.416 |
| | | Diet × weight ratio | 1, - | 1.510 | 0.219 |
| Rate of foreleg movements (/s) | Leg-arching | Diet | 1, 40 | 0.580 | 0.451 |
| | | Weight ratio | 1, 40 | 0.002 | 0.969 |
| | | Diet × weight ratio | 1, 40 | 0.000 | 0.995 |
| | Leg-extension | Diet | 1, 40 | 0.661 | 0.421 |
| | | Weight ratio | 1, 40 | 0.623 | 0.435 |
| | | Diet × weight ratio | 1, 40 | 2.136 | 0.152 |
| Lempel—Ziv complexity | Total seq. | Diet | 1, 40 | 1.973 | 0.168 |
| | | Weight ratio | 1, 40 | 1.305 | 0.260 |
| | | Diet × weight ratio | 1, 40 | 2.802 | 0.102 |
| | Leg-arching | Diet | 1, 37 | 0.328 | 0.570 |
| | | Weight ratio | 1, 40 | 1.624 | 0.210 |
| | | Diet × weight ratio | 1, 37 | 0.319 | 0.575 |
| | Leg-extension | Diet | 1, 40 | 2.768 | 0.104 |
| | | Weight ratio | 1, 40 | 0.344 | 0.561 |
| | | Diet × weight ratio | 1, 40 | 0.555 | 0.461 |
| Shannon entropy | Total seq. | Diet | 1, 40 | 4.821 | **0.034** |
| | | Weight ratio | 1, 40 | 0.028 | 0.868 |
| | | Diet × weight ratio | 1, 40 | 0.319 | 0.575 |
| | Leg-arching | Diet | 1, 37 | 0.014 | 0.908 |
| | | Weight ratio | 1, 37 | 0.198 | 0.659 |
| | | Diet × weight ratio | 1, 37 | 3.885 | 0.056 |
| | Leg-extension | Diet | 1, 40 | 1.677 | 0.203 |
| | | Weight ratio | 1, 40 | 0.483 | 0.491 |
| | | Diet × weight ratio | 1, 40 | 0.533 | 0.470 |
| Entropy rate | Total seq. | Diet | 1, 40 | 2.915 | 0.096 |
| | | Weight ratio | 1, 40 | 0.249 | 0.621 |
| | | Diet × weight ratio | 1, 40 | 0.476 | 0.494 |
| | Leg-arching | Diet | 1, 37 | 2.787 | 0.103 |
| | | Weight ratio | 1, 37 | 0.462 | 0.500 |
| | | Diet × weight ratio | 1, 37 | 0.329 | 0.569 |
| | Leg-extension | Diet | 1, 40 | 0.058 | 0.865 |
| | | Weight ratio | 1, 40 | 0.000 | 0.998 |
| | | Diet × weight ratio | 1, 40 | 0.058 | 0.811 |

*Statistically significant *P* values ($P < 0.05$) are denoted in bold.

(Fig. 9a). The interaction between diet and weight ratio significantly influenced the proportion of time spent in the leg-extension phase of the courtship display. Specifically, when the stimulus female was heavier than the male, high-diet males increased the proportion of time spent in the leg-extension phase. In contrast, low-diet males decreased the proportion of time spent in this phase as the females became relatively heavier.

However, the significant effects of interactions terms between diet and weight ratio may be driven by a single high-diet male (Fig. 9b). The removal of the outlier led to a decrease in the R-squared value by 10.6%, which suggests that the outlier had a significant effect on the model's ability to explain the variation in the leg-extension phase. Importantly, the *P* value for the interaction term between diet and weight ratio changed from 0.025 in the full model to 0.462 in the filtered model, indicating that the outlier was driving the statistical significance of the interaction effect. Additionally, the coefficients for the interaction term between diet and weight_ratio showed a shift, with the effect size changing from $\beta = -0.091$ in the full model to $\beta = 0.028$ after filtering the outlier.

### *Binary similarity measures*

Agglomerative clustering based on DTW distance among temporal sequences of GHMM states found three clusters of the foreleg movements of *R. rabida* males (Fig. 10). The multinomial logistic regression showed that male diet can predict the clustering results ($F_{2,\,80} = 3.349$, $P = 0.040$), whereas the weight ratio between males and females and the interaction term cannot (weight ratio: $F_{2,\,80} = 0.053$, $P = 0.949$; interaction term: $F_{2,\,80} = 0.359$, $P = 0.700$). Cluster 1 and Cluster 3 included more high-diet males than low-diet males (Clusters 1—14 versus 2; Clusters 3—12 versus 3), whereas Cluster 1 included more low-diet males than high-diet males (Clusters 2—4 versus 9; Fig. 10).

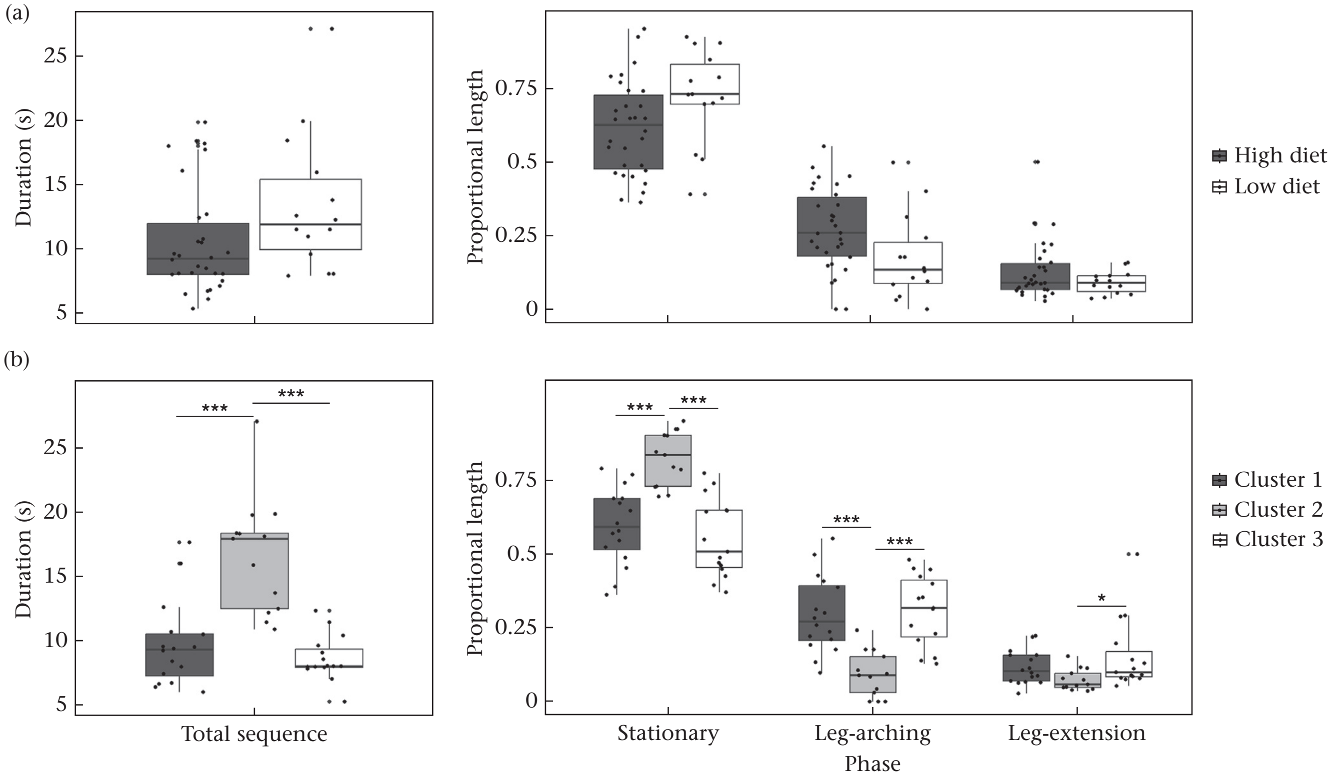

**Figure 6.** The duration of total foreleg movements (left) and each phase (right). (a) Comparison between low- and high-diet males. (b) Comparison between clusters of male foreleg movements based on binary similarity measure. The top, middle and bottom of the box represent the 25th, 50th and 75th percentiles, respectively. The whiskers represent 1.5 times the IQR or the most extreme value. Statistically significant differences are denoted by asterisks (*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$).

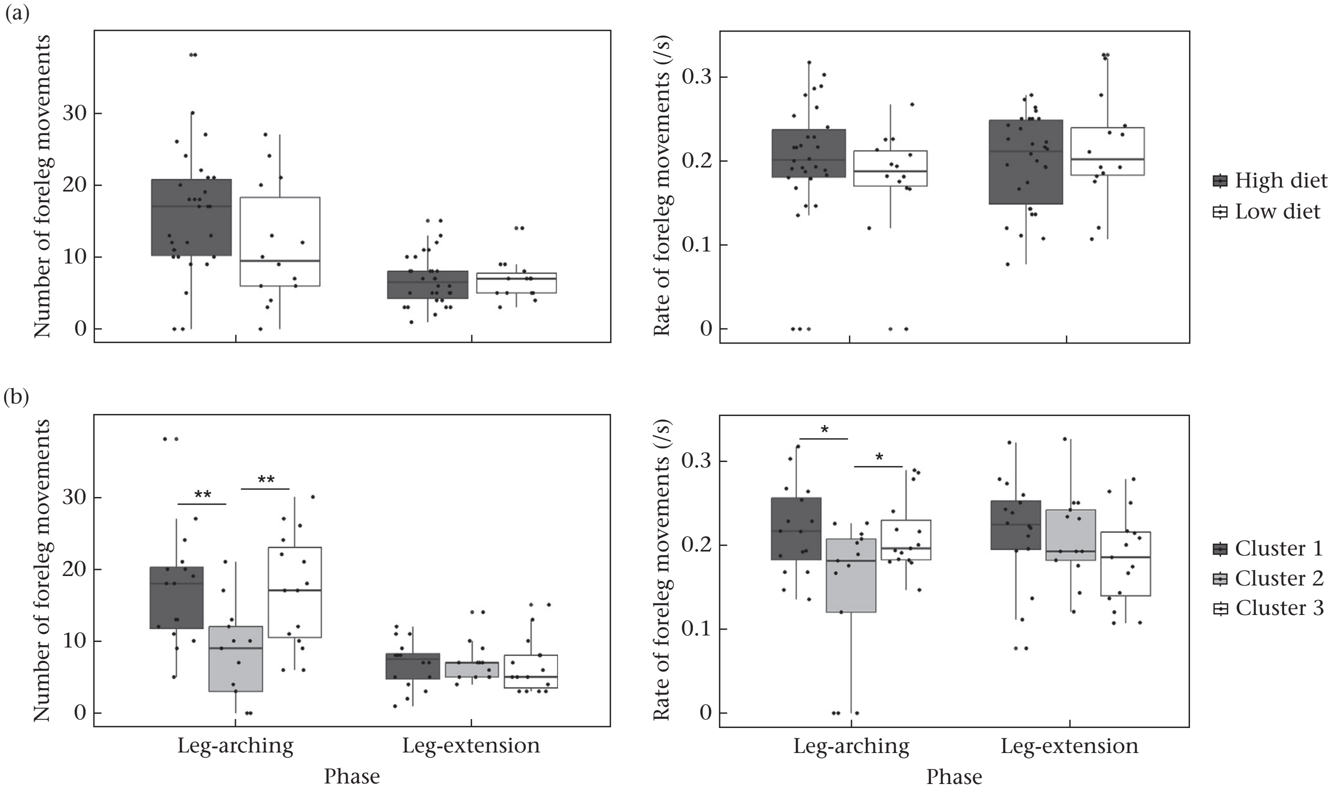

**Figure 7.** The number (left) and rate (right) of foreleg movements during leg-arching and leg-extension phases. (a) Comparison between low- and high-diet males. (b) Comparison between clusters of male foreleg movements based on binary similarity measure. The top, middle and bottom of the box represent the 25th, 50th and 75th percentiles, respectively. The whiskers represent 1.5 times the IQR or most extreme value. Statistically significant differences were denoted by asterisks (*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$).

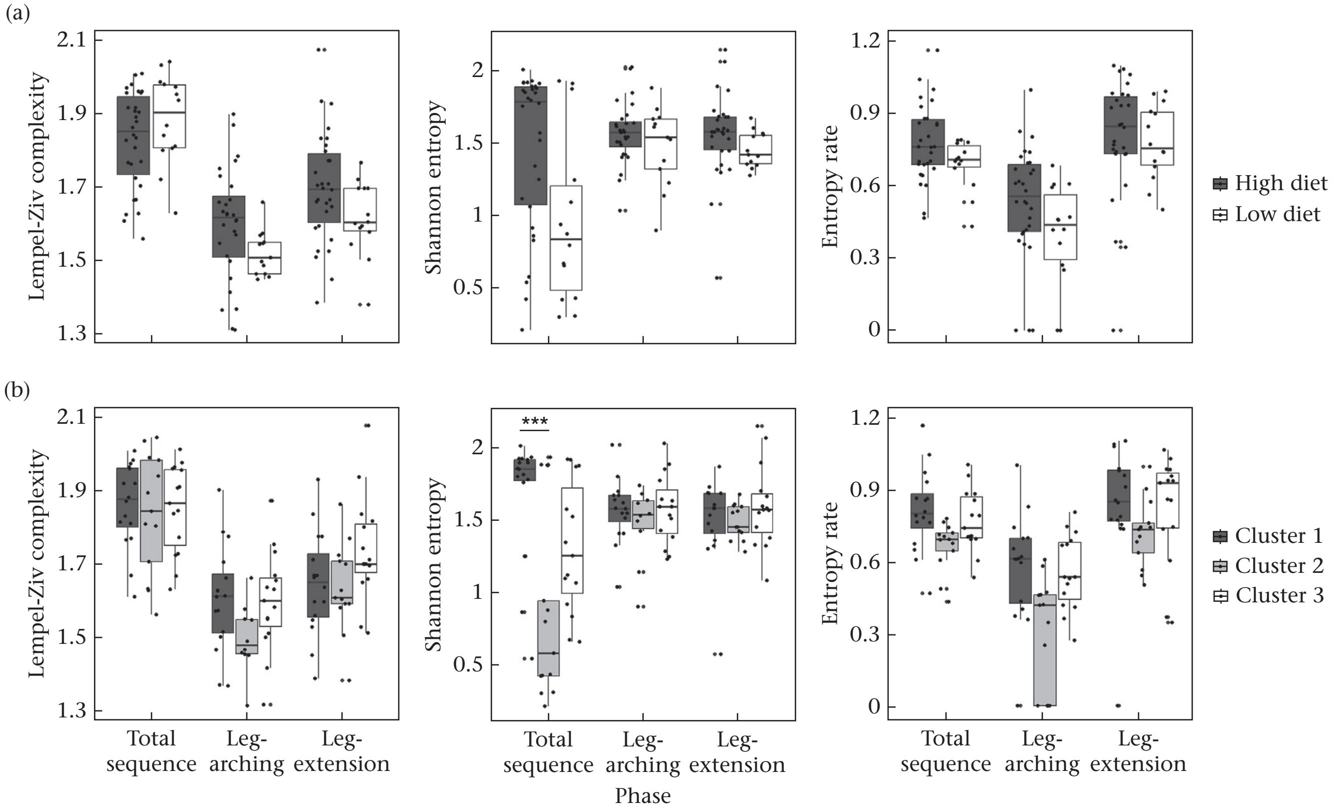

**Figure 8.** The Lempel–Ziv complexity (left), Shannon entropy (centre) and entropy rate (right) of total foreleg movements, leg-arching phase and leg-extension phase. (a) Comparison between low- and high-diet males. (b) Comparison between clusters of male foreleg movements based on binary similarity measure. The top, middle and bottom of the box represent the 25th, 50th and 75th percentiles, respectively. The whiskers represent 1.5 times the IQR or most extreme value. Statistically significant differences were denoted by asterisks (*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$).

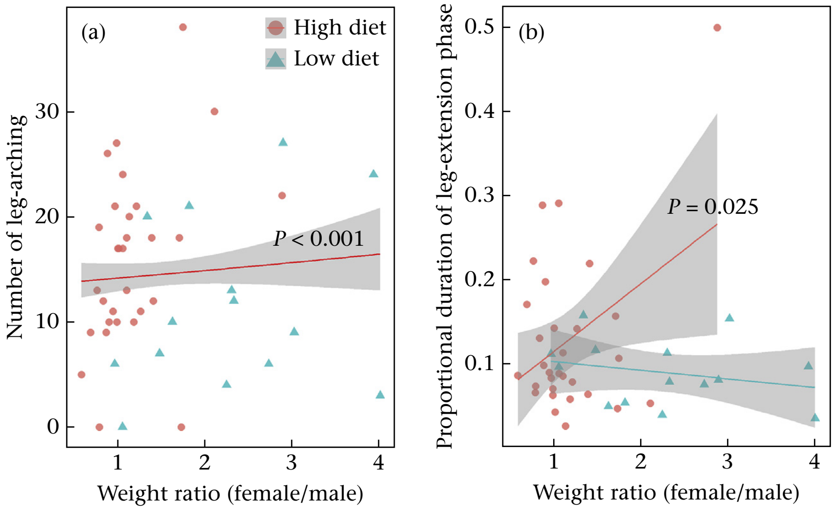

**Figure 9.** The effect of body weight ratio (female/male) and the interaction term between male diet and body weight ratio on male foreleg movement. (a) The effect of body weight ratio on the number of leg-arching behaviours. (b) The effect of the interaction term on the proportion of the leg-extension phase in a total foreleg movement. However, this effect was no longer significant after removing the outlier ($P = 0.462$). $P$ values were denoted on the figure.

### *Combination of unary and binary similarity measures*

The cluster to which male courtship display belongs predicts (1) the duration of total, stationary, leg-arching and leg-extension phases, (2) the number and rate of leg-arching postures, (3) the Shannon entropy of total visual courtship display and (4) entropy rate of the leg-extension phase (Table 2). Male foreleg movements in Cluster 2 showed significantly (1) longer stationary phase and shorter leg-arching and leg-extension phases than Cluster 1 and Cluster 3 (Fig. 6b), (2) fewer numbers of leg-arching postures with slower rates than Cluster 1 and Cluster 3 (Fig. 7b) and (3) less complexity in terms of the proportion of different foreleg postures (i.e. Shannon entropy) than Cluster 1 (Fig. 8b). However, there was no significant pairwise difference among the clusters in entropy rates. Cluster 1 and Cluster 3 were not significantly different in all

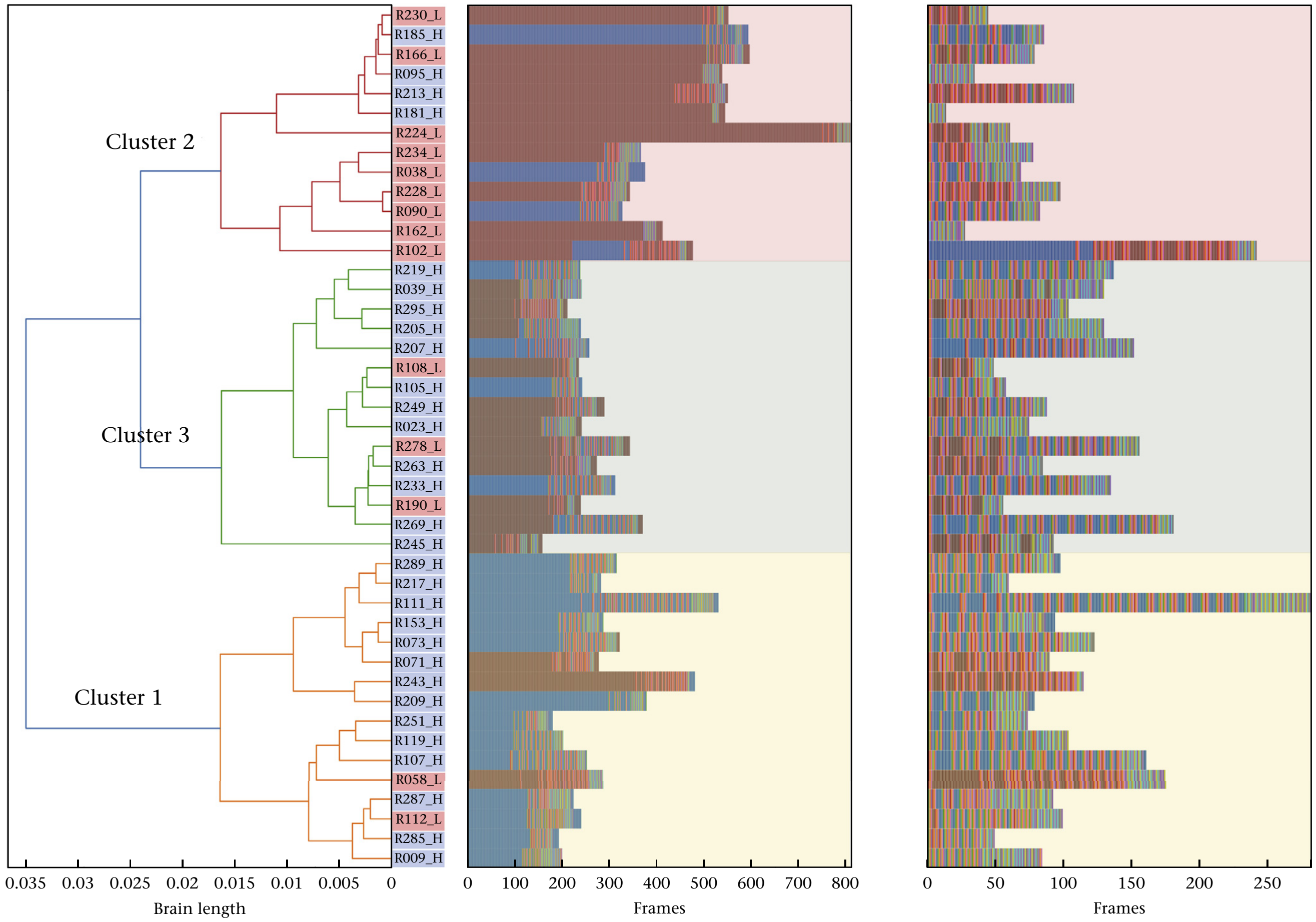

**Figure 10.** The dendrogram of the binary similarity measures of male foreleg movements (left) with the temporal sequence of total foreleg movements (centre) and after the stationary phase (right). The low- (red) and high-diet (blue) males and different clusters (Cluster 1: yellow; Cluster 2: red; Cluster 3: green) are colour-coded.

features, but the posture during the stationary phase (Posture 0 versus Posture 5; Fig. 10).

The regression models explained variations in male foreleg movements more effectively when using clusters based on pairwise DTW distances as predictor variables rather than male diet treatment (Table 3).

## DISCUSSION

This study documents diet-dependent dynamic visual courtship displays in the wolf spider *R. rabida*. The results contribute to our growing knowledge of complex signal functions in this species and build on our foundation of previously documented diet-dependent signalling components (i.e. vibratory signalling, Wilgers & Hebets, 2012a; static visual signalling or foreleg ornamentation, Wilgers & Hebets, 2011). Using a ‘bottom-up approach’ that leveraged GHMM, we were able to successfully define the structural organization of foreleg movements in an automated and reproducible manner. Furthermore, by implementing both a traditional unary approach and a newer binary approach, we were able to determine that our computational approach is comparable with results based solely on human observers. Ultimately, combining unary similarity measures with binary similarity measures provided us with a powerful approach for quantifying and interpreting diet-dependent dynamic visual signalling, setting the stage for future studies exploring its specific role(s) in mate choice.

Across both similarity measures (unary and binary measures) and their combination, our results showed that the prior foraging history of male *R. rabida* influenced the foreleg movements during courtship displays. Low-diet males (1) increased the duration of their foreleg movements, (2) increased the proportion of the stationary phase and (3) reduced the proportion of leg-arching behaviours with a slower rate, whereas there was (4) no significant variation in the leg-extension phase (Figs. 3 and 10). In general, low-diet males produced slower dynamic foreleg movements with a longer stationary phase. The longer stationary phase, which consists of a single foreleg posture, reduces the Shannon entropy of the foreleg movement of low-diet males (Fig. 8). With a higher Shannon entropy score, high-diet males engage in more complex courtship displays in terms of the diversity of foreleg postures consisting of the foreleg movements (Fig. 10).

Previous studies on the multimodal courtship display of *R. rabidosa* suggested that vibratory displays and static visual displays (i.e. foreleg ornamentation) can indicate a male’s past foraging success (Wilgers & Hebets, 2011; 2012a). Our results similarly suggest that the dynamic visual display (i.e. foreleg movement), alongside vibratory signalling and static visual signalling, also provides information regarding male quality. Interestingly, however, the variation in the effects of diet manipulation on different dynamic components (leg-arching versus leg-extension phases) of male foreleg movements suggests that different components may serve different functions. Thus, within the dynamic visual display, there may be specific movements that

**Table 2**
The results of regression models of the unary similarity measures with predictors including clusters based on a binary similarity measure (i.e. DTW distance), the weight ratio between female and male spiders and the interaction term

| Dependent variable | Phase | Predictor(s) | *df* | *F* | *P* |
|---|---|---|---|---|---|
| Duration | Total seq. | Cluster | 2, 38 | 17.340 | **<0.001** |
| | | Weight ratio | 1, 38 | 1.398 | 0.244 |
| | | Cluster × weight ratio | 2, 38 | 0.182 | 0.834 |
| | Stationary | Cluster | 2, 38 | 20.670 | **<0.001** |
| | | Weight ratio | 1, 38 | 2.220 | 0.144 |
| | | Cluster × weight ratio | 2, 38 | 1.648 | 0.206 |
| | Leg-arching | Cluster | 2, 38 | 17.446 | **<0.001** |
| | | Weight ratio | 1, 38 | 3.691 | 0.062 |
| | | Cluster × weight ratio | 2, 38 | 2.039 | 0.144 |
| | Leg-extension | Cluster | 2, 38 | 3.241 | **0.050** |
| | | Weight ratio | 1, 38 | 0.349 | 0.558 |
| | | Cluster × weight ratio | 2, 38 | 0.310 | 0.735 |
| Number of foreleg movements | Leg-arching | Cluster | 2, - | 22.549 | **<0.001** |
| | | Weight ratio | 1, - | 5.995 | **0.014** |
| | | Cluster × weight ratio | 2, - | 1.399 | 0.247 |
| | Leg-extension | Cluster | 2, - | 0.206 | 0.814 |
| | | Weight ratio | 1, - | 0.080 | 0.778 |
| | | Cluster × weight ratio | 2, - | 0.725 | 0.484 |
| Rate of foreleg movements (/s) | Leg-arching | Cluster | 2, 38 | 5.982 | **0.006** |
| | | Weight ratio | 1, 38 | 0.111 | 0.741 |
| | | Cluster × weight ratio | 2, 38 | 1.324 | 0.278 |
| | Leg-extension | Cluster | 2, 38 | 1.715 | 0.194 |
| | | Weight ratio | 1, 38 | 0.039 | 0.844 |
| | | Cluster × weight ratio | 2, 38 | 1.214 | 0.308 |
| Lempel–Ziv complexity | Total seq. | Cluster | 2, 38 | 0.696 | 0.505 |
| | | Weight ratio | 1, 38 | 0.137 | 0.713 |
| | | Cluster × weight ratio | 2, 38 | 4.260 | **0.021** |
| | Leg-arching | Cluster | 2, 35 | 1.834 | 0.173 |
| | | Weight ratio | 1, 35 | 1.425 | 0.241 |
| | | Cluster × weight ratio | 2, 38 | 0.877 | 0.425 |
| | Leg-extension | Cluster | 2, 38 | 2.193 | 0.126 |
| | | Weight ratio | 1, 38 | 0.389 | 0.537 |
| | | Cluster × weight ratio | 2, 38 | 0.131 | 0.877 |
| Shannon entropy | Total seq. | Cluster | 2, 38 | 8.464 | **<0.001** |
| | | Weight ratio | 1, 38 | 0.476 | 0.495 |
| | | Cluster × weight ratio | 2, 38 | 0.675 | 0.515 |
| | Leg-arching | Cluster | 2, 35 | 0.027 | 0.973 |
| | | Weight ratio | 1, 35 | 1.739 | 0.196 |
| | | Cluster × weight ratio | 2, 38 | 1.527 | 0.231 |
| | Leg-extension | Cluster | 2, 38 | 0.781 | 0.465 |
| | | Weight ratio | 1, 38 | 0.068 | 0.795 |
| | | Cluster × weight ratio | 2, 38 | 0.162 | 0.851 |
| Entropy rate | Total seq. | Cluster | 2, 38 | 2.915 | 0.096 |
| | | Weight ratio | 1, 38 | 0.031 | 0.860 |
| | | Cluster × weight ratio | 2, 38 | 0.051 | 0.951 |
| | Leg-arching | Cluster | 2, 35 | 6.071 | 0.699 |
| | | Weight ratio | 1, 35 | 0.151 | 0.699 |
| | | Cluster × weight ratio | 2, 38 | 0.219 | 0.804 |
| | Leg-extension | Cluster | 2, 38 | 3.327 | **0.047** |
| | | Weight ratio | 1, 38 | 0.041 | 0.841 |
| | | Cluster × weight ratio | 2, 38 | 0.044 | 0.957 |

*Statistically significant *P* values ($P < 0.05$) are denoted in bold.

are selected for different functions, suggesting multivariate selection on the evolution of multicomponent dynamic visual courtship displays. Further research is needed to explore this multivariate selection further, although we provide some discussion on this in the following paragraphs. Regardless, such future research will require the ability to manipulate dynamic visual displays; another outstanding challenge in understanding complex animal communication.

The leg-arching phases showed clear diet-dependence, with high-diet males displaying more leg-arching. This phase of courtship may be physically demanding as it involves repeated up and down movements of whole foreleg segments (Rovner, 1968). A study on another wolf spider system directly demonstrated increased energetic costs associated with visual displays (*Schizocosa ocreata*, Cady et al., 2011). The lack of sufficient energy from the reduced quantity diet of low-diet males may thus have prevented them from producing these longer foreleg movements. Unlike the leg-arching phase, however, there was no difference in leg-extension phases between high and low-diet males, although low-diet males decreased leg-extensions with heavier females. The distinct action patterns of leg-arching and leg-extension phases [up and down versus pushing forward; see .gif files in the Dryad repository (Choi et al., 2025)] suggest that two foreleg movements may differ in the energy demands for production and thus may provide different information regarding a signaller's energy resources. Future research, however, is required to rigorously compare the metabolic cost of leg-arching versus leg-extension phases.

Alternatively, low-diet males may decrease the frequency of leg-arching behaviour, which appears to be the most conspicuous component, to mitigate the risk of being cannibalized by non-receptive females (Persons & Uetz, 2005; Wilgers et al., 2009;

**Table 3**

Model comparison of regression models with male diet (Diet) and cluster of foreleg movements (Cluster) with other predictors (weight ratio and the interaction term)

| Variable | Phase | AIC | | BIC | | $R^2$ | | Adjusted $R^2$ | |
|---|---|---|---|---|---|---|---|---|---|
| | | Diet | Cluster | Diet | Cluster | Diet | Cluster | Diet | Cluster |
| Duration | Total sequence | 265.257 | **239.425** | 274.178 | **251.914** | 0.121 | **0.554** | 0.055 | **0.495** |
| | Stationary | **−30.563** | **−56.209** | **−21.642** | **−43.719** | **0.137** | **0.560** | **0.073** | **0.502** |
| | Leg-arching | **−42.654** | **−63.878** | **−33.733** | **−51.389** | **0.167** | **0.530** | **0.104** | **0.469** |
| | Leg-extension | −91.428 | **−86.419** | −82.507 | **−73.930** | 0.183 | **0.164** | 0.122 | **0.055** |
| Number of foreleg movements | Leg-arching | **314.370** | **309.028** | **323.291** | **321.518** | **0.167** | **0.326** | **0.105** | **0.238** |
| | Leg-extension | 235.110 | 239.069 | 244.031 | 251.558 | 0.028 | 0.029 | −0.045 | −0.099 |
| Rate of foreleg movements (/s) | Leg-arching | −102.582 | **−111.106** | −93.661 | **−98.616** | 0.021 | **0.264** | −0.052 | **0.167** |
| | Leg-extension | −119.755 | −117.992 | −110.834 | −105.503 | 0.068 | 0.115 | −0.001 | −0.002 |
| Lempel−Ziv complexity | Total sequence | −51.064 | −51.191 | −42.143 | −38.701 | 0.112 | 0.192 | 0.046 | 0.085 |
| | Leg-arching | −43.353 | −43.268 | −34.785 | −31.273 | 0.112 | 0.193 | 0.040 | 0.078 |
| | Leg-extension | −43.047 | −40.546 | −34.126 | −28.057 | 0.094 | 0.124 | 0.026 | 0.009 |
| Shannon entropy | Total sequence | **80.929** | **73.466** | **89.850** | **85.955** | **0.166** | **0.357** | **0.103** | **0.272** |
| | Leg-arching | −0.537 | 3.684 | 8.031 | 15.679 | 0.148 | 0.143 | 0.079 | 0.021 |
| | Leg-extension | 8.860 | 13.324 | 17.781 | 25.813 | 0.058 | 0.048 | −0.013 | −0.078 |
| Entropy rate | Total sequence | −38.516 | −38.146 | −29.595 | −25.657 | 0.100 | 0.171 | 0.032 | 0.062 |
| | Leg-arching | 2.315 | −3.610 | 11.236 | 8.879 | 0.083 | 0.268 | 0.014 | 0.172 |
| | Leg-extension | −0.572 | **1.008** | 8.349 | **13.498** | 0.004 | **0.057** | −0.071 | **−0.067** |

*The model significance is denoted by bold.

Wilgers & Hebets, 2012a). In previous experiments, Wilgers and Hebets (2012a, 2012b) showed that low-diet males (1) produced longer introductory vibratory signals before dynamic visual signals and (2) were more likely to be cannibalized. Thus, if males are not in the 'acceptable' range of body conditions to the encountered females, they may show a longer stationary phase to assess the potential risk of cannibalism and a shorter leg-arching phase in response to negative feedback from nonreceptive females. Sullivan-Beckers and Hebets (2014) also proposed that this tactical and plastic adjustment of male courtship displays not only enhances mating success but also reduces aggression from females in *Schizocosa rovneri* wolf spiders. Unfortunately, we did not record vibratory signals during experiments to verify whether the longer stationary periods of foreleg movements are associated with the longer production of introductory vibratory signals.

As mentioned previously, the leg-extension phase did not vary due to male diet treatment, opening the possibility of this display component serving a different function. For instance, the leg-arching phase may draw the females' attention and convey information about the signaller's quality with conspicuous and energetically costly behaviour, whereas the leg-extension may function to reduce the risk of potential cannibalism through some additional mechanisms [e.g. sensory overload (Belkina et al., 2021; Hebets & Papaj, 2005; Herberstein et al., 2014)]. Although this specific hypothesis has not yet been tested in *R. rabida*, in the orb-web spider *Argiope keyserlingi*, one component of male vibratory signals (shuddering behaviour) functions to reduce postcopulatory cannibalization by females (Wignall & Herberstein, 2013). It is also possible that leg-extension itself does not serve a function but is simply a necessary motion for successfully producing a full foreleg movement. Future biomechanics studies are required to assess this possibility.

Ultimately, our study demonstrates the effect of prior foraging history on aspects of dynamic visual signalling, specifically leg-arching. Possessing the potential to convey information, however, and being selected for information transmission are two different things. In *R. rabida*, for example, despite the fact that vibratory and visual signalling (combined ornamentation and foreleg movement) are indicators of past diet and are sufficient for successful mating (Wilgers & Hebets, 2012a), females only appear to use variation in ornamentation in their mating decisions in the presence of vibratory signals (Wilgers & Hebets, 2011; 2012b). Such interactions between signalling modalities are not uncommon (see Hebets & Papaj, 2005; Reichert & Höbel, 2015; Stange et al., 2017), yet are often challenging to identify and study. Also, the significant variation in foreleg lengths between high- and low-diet males suggests further interactions with other nonsignalling cues that reflect the body condition of signallers. The next steps in understanding the full complex courtship signalling of *R. rabida* will require studies aimed at determining how variation in dynamic visual signalling influences male mating success (and thus female choice), both in isolation and in combination with the full multimodal courtship display.

In addition to documenting diet-dependent effects, we also found evidence of plasticity in the dynamic visual courtship displays of male *R. rabida*. This is not the first time that researchers have observed variability in this species' dynamic signalling. For example, males have been shown to reduce visual signalling when signal transmission is impaired (Wilgers & Hebets, 2011). Our study now demonstrates that males adjust their courtship displays in response to female characteristics. Although the relationship between female body condition and fecundity has not been explicitly tested in *R. rabida*, Moskalik and Uetz (2016) found that well-fed *S. ocreata* wolf spider females matured faster, produced more eggs, and were more likely to be receptive. This suggests that males may assess females before initiating courtship and may modulate their signalling effort based on the estimated fecundity or receptivity of potential mates. Although we specifically examined the effects of female body weight, males may also assess other traits correlated with female body condition, such as body size.

Beyond the potential reproductive benefits of signalling to heavier females, adjusting courtship effort based on female weight may also help males manage signalling costs. Previous studies on *Schizocosa* wolf spiders suggest that multimodal courtship (visual + vibratory signalling) can be energetically costly (Cady et al., 2011) or increase the risk of eavesdropping by predators or rival males (*S. ocreata*, Hoefler et al., 2008; Pruden & Uetz, 2004). If lighter females are perceived as less fecund, males may strategically reduce their courtship effort to conserve energy. Additionally, courting nonreceptive females in poor condition could increase the risk of premating cannibalism (Persons & Uetz, 2005).

Regarding our comparison between unary and binary approaches to signal quantification, our regression models explained the variations in male foreleg movements more effectively when the predictor variables included clusters based on pairwise DTW distances rather than the male diet treatment (Table 3). The lower explanatory power of regression models with the male diet treatments as a predictor variable may be due to the presence of 'outlier' males that produced foreleg movements different from other males with the same diet treatment. By the agglomerative clustering with the pairwise similarities, 4 of 30 high-diet males and 5 of 14 low-diet males were clustered to different clusters with the majority of the males with the same diet treatment (Fig. 10). The regression models with diet treatment as a predictor assume that the same diet treatment is likely to elicit similar behavioural responses from the males. Although this assumption may hold with large sample size, it can be violated by individual-level variation in a small sample and by suboptimal feature selection, where irrelevant variables are included or important ones are excluded, potentially leading to inaccurate model results. The better explanatory power of the regression models through the combination of unary and binary similarities measures may provide an efficient method to achieve biologically meaningful comparisons of animal behaviours even with the small sample size by pairwise comparison of animal signals based on binary similarities, which are not constrained by the number and quality of features for unary similarity measurements.

Ultimately, through GHMM, we successfully identified the structural organization of male foreleg movement from the smallest possible unit, a foreleg posture during a single video frame (~ 30 ms), to the major phases of foreleg movements (stationary, leg-arching and leg-extension) including different motifs. In particular, the occurrence patterns of foreleg postures are highly stereotyped in terms of the transition between postures and the positions of the motifs within a total sequence of foreleg movement (Figs. 3 and 4). Also, the motifs from our bottom-up approach are comparable with the previous description of signal components and transition patterns of the visual courtship display of *R. rabida* (Rovner, 1968). Given the comparability with the manual definition of signal components (Rovner, 1968), our results showed that the bottom-up definition of structural organization can be an efficient tool for (1) an automated alternative to the manual ethogram-based annotation of complex animal signals and (2) a framework for reproducible and updatable research on the communication of understudied species by unsupervised algorithms.

The methodological innovation described herein does not imply the replacement of expert knowledge (e.g. manual ethograms) but rather transfers the accumulated knowledge into more accessible, reproducible and updatable information for a better understanding of the evolution of complex animal behaviour, including communication. For instance, both manual and automated approaches often require fine-tuning to optimize the efficiency when they add or use new data sets from different experimental settings (e.g. camera angle, lighting and size of objects). When researchers use manually defined ethograms, regardless of adequacy, it is often difficult to explain why and how an individual expert did such fine-tuning to other researchers. However, with the automated bottom-up approach, experts can modify the machine learning models through the validation of the hyperparameters with their experience and knowledge about the study system (e.g. the exploration range of the optimal GHMM and target motif size for MEME), and other researchers can easily reproduce the process to validate the modification. By integrating this bottom-up framework, we propose that a data-driven approach to complex animal signals can help overcome traditional obstacles by (1) introducing reproducible analysis pipelines in behavioural research and (2) providing metrics that minimize bias introduced by individual feature selection (e.g. binary similarity measures).

## Author Contributions

**Noori Choi:** Writing – original draft, Visualization, Software, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Eileen A. Hebets:** Writing – review & editing, Supervision, Project administration, Investigation, Funding acquisition, Conceptualization. **Dustin J. Wilgers:** Writing – review & editing, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization.

## Data Availability

The data set and code for this paper are available at https://10.5061/dryad.mgqnk9989. See Choi et al. (2025).

## Declaration of Interest

Authors declare that they have no competing interests.

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## Supplementary Material

Supplementary material associated with this article is available at https://doi.org/10.1016/j.anbehav.2025.123226.

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