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Sex-specific life-history strategies among immature jumping spiders: Differences in body parameters and behavior

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Abstract

Selection forces often generate sex-specific differences in various traits closely related to fitness. While in adult spiders (Araneae), sexes often differ in coloration, body size, antipredator, or foraging behavior, such sex-related differences are less pronounced among immatures. However, sex-specific life-history strategies may also be adaptive for immatures. Thus, we hypothesized that among spiders, immature individuals show different life-history strategies that are expressed as sex-specific differences in body parameters and behavioral features, and also in their relationships. We used immature individuals of a protandrous jumping spider, *Carrhotus xanthogramma*, and examined sex-related differences. The results showed that males have higher mass and larger prosoma than females. Males were more active and more risk tolerant than females. Male activity increased with time, and larger males tended to capture the prey faster than small ones, while females showed no such patterns. However, females reacted to the threatening abiotic stimuli more with the increasing number of test sessions. In both males and females, individuals with better body conditions tended to be more risk averse. Spiders showed no sex-specific differences in interindividual behavioral consistency and in intraindividual behavioral variation in the measured behavioral traits. Finally, we also found evidence for behavioral syndromes (i.e., correlation between different behaviors), where in males, only the activity correlated with the risk-taking behavior, but in females, all the measured behavioral traits were involved. The present study demonstrates that *C. xanthogramma* sexes follow different life-history strategies even before attaining maturity.

Key words: activity, behavioral syndrome, boldness, intraindividual variability, repeatability, sexual dimorphism

Animals often face life-history trade-offs during their lifetime due to different internal or external constraints, generating inter- and intraspecific variations in traits that are tightly linked with their fitness (Alonzo and Kindsvater 2008; Chapin 2017). Differential reproductive investment among sexes can also generate variability (regarding many fitness-related traits) among individuals. Therefore, due to their different investment, sexes may face different selection pressures, resulting in physiological, morphological, and behavioral differences (Slatkin 1984). Sexually dimorphic traits are shaped either by sexual selection or by natural selection. However, many traits are often exposed simultaneously to both forms of selective forces (Hosken and House 2011). Generally, the effect of net selection (sum of selection forces) is stronger in males (Winkler et al. 2021). This seems to allow populations to adapt faster to new environmental challenges (Winkler et al. 2021). Therefore, selection may shape the traits of females and males in different ways resulting in sex-specific life histories across several interlinked traits (Hämäläinen et al. 2018; Tarka et al. 2018).

Animal behavior can be an adaptive and flexible response to various ecological and environmental challenges and can directly affect specific fitness components (Moiron et al.

2020). Recently, an increasing number of studies have focused on behavioral ecology of different arthropod taxa, including spiders, to understand inter- and intraindividual behavioral variations and behavioral correlations (i.e., behavioral syndromes) (Kralj-Fišer and Schuett 2014; Modlmeier et al. 2015). Similarly to vertebrates, certain arthropod taxa have consistent interindividual behavioral differences (also referred to as animal personality: the temporal variation of the same behavioral trait) (Bell et al. 2009; Réale and Dingemanse 2012). Behavioral consistency (in one behavior and/or among correlated behaviors) might favor individuals and, through them, populations or species in an adaptive manner, depending on the current ecological situation (Dingemanse and Réale 2005; Réale and Dingemanse 2012; Jandt et al. 2014). However, compared with vertebrates, this phenomenon in arthropods has received much less attention. Nevertheless, some good examples emphasize the adaptive significance of consistent behavioral differences in certain spider species as compared to other species. *Larinioides sclopetarius* (Araneidae) easily colonize urban habitats, possibly due to personality, that is, consistent boldness and increased activity in a novel environment (Kralj-Fišer and Schneider 2012; Kralj-Fišer et al. 2017). Besides this, certain arthropod taxa

can form behavioral syndromes when behavioral traits measured in 2 or more functionally different ecological situations/contexts correlate with each other (Sih et al. 2004; Royauté et al. 2014; Michalko et al. 2017). For example, in a fishing spider (*Dolomedes triton*, Pisauridae), voracity toward heterospecific prey often positively correlates with precopulatory sexual cannibalism. Although consuming potential mates is not necessarily adaptive, it seems that high levels of voracity (in different situations) can improve the fitness of spiders by increasing their adult size and fecundity (Johnson and Sih 2005). Apart from this, some level of behavioral plasticity that allows individuals of a species to react rapidly to an emerging environmental challenge by altering behavior can also be advantageous (Dingemanse and Réale 2005; Snell-Rood 2013). Sometimes individuals show high similarity in the behavioral mean, but there may be individual differences in behavioral predictability (Stamps et al. 2012). For example, in an araneophagous jumping spider, *Portia labiata* (Salticidae), the intraindividual variability (IIV) in boldness may increase in the presence of a conspecific (Chang et al. 2019). Higher IIV in a behavior indicated lower predictability (i.e., individuals behave less consistently), which may be more advantageous for *P. labiata* in a dangerous situation (Chang et al. 2019). These examples indicate that arthropods, particularly spiders, are suitable model organisms to provide a unique insight into behavioral variations.

Among spiders, sexual dimorphism is very common in several features such as morphology, behavior, and life history. Sex-specific morphological and behavioral traits can be genetically determined (Kralj-Fišer et al. 2019, 2021; Chang et al. 2020; Cordellier et al. 2020) and generate specific consequences for life history. For example, spiders usually practice protandry, that is, a male matures earlier and has a shorter lifespan than a female (Klein 1988; Uhl et al. 2004; Foelix 2011; Kralj-Fišer et al. 2014). Sexual maturation can often change the males' appearance and behavior (Sullivan and Morse 2004; Framenau 2005; Cordellier et al. 2020). Besides these differences, there are sex-specific variations in metabolic rate (Kotiaho 1998), immune response (Rádai et al. 2018), body size (Head 1995; Prenter et al. 1998), or other morphological traits (Albín et al. 2018). Furthermore, spiders exhibit sexual dimorphism in features related to behavioral ecology, for example, in aggressiveness (Kralj-Fišer et al. 2017, 2019), boldness (Sweeney et al. 2013), the behavioral mean, and even in the temporal pattern of locomotor activity (Schmitt et al. 1990; Krumpálová and Tuf 2013; Mezőfi et al. 2019).

Most behavioral studies of invertebrates have focused on adult individuals where sex-specific differences (e.g., morphological traits) are clearly expressed. However, a few studies have shown that the manifested behavioral traits may not always be the same during the individual lifespan as behavioral trait expression can change with development and experience (Carducci and Jakob 2000; Dingemanse et al. 2010; DiRienzo and Montiglio 2016). For example, the effect of the environment played an essential role in shaping behavioral traits in *Marpissa muscosa* (Salticidae). Individuals of this species grown in a physically enriched environment tended to be more exploratory (Liedtke et al. 2015), while social enrichment improved their cognitive abilities (Liedtke and Schneider 2017). These studies highlight the relationship between environmental conditions and behavioral flexibility during the ontogeny of immature spiders, but there is still a knowledge gap on the sex-related differences in immature stages.

The protandrous jumping spider, *Carrhotus xanthogramma* (Latreille, 1819), is a euryphagous species that is widely distributed from Europe to the Far East and can be the dominant hunting spider in the canopy level of pome fruit orchards (Mezőfi et al. 2020; WSC 2021). Although the immature stages have a fairly similar pattern and coloration, adults show marked sexual dimorphism in these features (males are much darker than females, but the opisthosoma of males is usually a richer red brown), and according to Kim and Lee (2014), males are generally slightly shorter in body length. Additionally, a recent study found sex-related behavioral differences in adults: Females were more active than males (Mezőfi et al. 2019).

Therefore, we aimed to detect sex-specific differences regarding the most crucial fitness-related traits in the seemingly uniform immature individuals (i.e., penultimate and antepenultimate instars) of our chosen model organism, *C. xanthogramma*. We tested for sex-specific differences in some body parameters and behavioral variability across time (both at inter- and intraindividual levels) and functionally different ecological situations (i.e., behavioral syndrome). We supposed that sex-specific differences might already be expressed before maturity due to genetically determined physiological background (i.e., sex-specific life-history trade-offs). In that case, we expected sex-specific differences in some specific fitness-related traits and their correlation structure. Finally, we also tested the relationship between body parameters and behavioral traits. If any sex-specific differences were detected regarding the body parameters or behavior, we also predicted a close link among these traits suggesting sex-specific differences in the life-history trade-off structure.

Materials and Methods

Test animals and animal housing

We collected *C. xanthogramma* individuals from 3 insecticide-free apple orchards, that is, from 3 spatially isolated *C. xanthogramma* populations. We labeled the sampling sites by their closest village as follows: Csány ("Site_Cs", 47°38′25″N, 19°46′24″E) and Madocsa ("Site_M1", 46°40′42″N, 18°58′21″E; "Site_M2", 46°40′48″N, 18°58′31″E). Both Site_Cs and Site_M1 had been abandoned for several years, while the orchard Site_M2 was sprayed yearly with a contact fungicide combination (Vegesol-eReS, BVN Növényvédő Ltd., active ingredients: copper hydroxide + sulfur + sunflower oil, dose: 5 L/ha, applied: 12 April 2017) and here, the vegetation between the rows was mown 2 times a year. All the sampled sites were surrounded by other apple orchards and crop fields.

We collected 31, 31, and 30 immature (mainly penultimate) individuals by beating the branches of randomly chosen apple trees between the 11 and 15 of September 2017 in Site_Cs, Site_M1, and Site_M2, respectively. For the beating, we used a beating funnel 70 cm in diameter and a ~120-cm-long beating stick, and we collected the spiders that fell from the tree. In the laboratory, we housed the collected spiders individually in plastic Petri dishes (height: 16 mm, outer diameter: 61 mm) and placed them in random order on plastic trays after labeling them by a specific ID. We covered the sides of the Petri dishes with white tape to avoid possible disturbance from spiders in the neighboring Petri dishes. On 20 September 2017, we placed and thereafter kept the spiders in our behavioral laboratory in a standard environment (temperature

[mean, ±standard deviation {SD}]: 19.26 °C, ± 1.39 °C; relative humidity [mean, ± *SD*]: 42.26%, ±5.41%; photoperiod [L:D]: 16:8 h). To synchronize their hunger level, on the first acclimatization day (21 September 2017), we fed each spider with 3 flightless fruit flies *Drosophila hydei*. Apart from this, the spiders received food only during the behavioral assays (see later), resulting in controlled hunger levels in all sessions. Additional water supply was restricted during the experiments to keep the relative humidity low because *C. xanthogramma* mainly prefers sunny and dry habitats (Szinetár 2006). We started the behavioral assays on 26 September 2017, so the spiders had enough time to acclimatize to the new conditions in the behavioral laboratory.

A few days before the first behavioral assay session (on the 18th of September) and after the last (on the 24th of October) behavioral assay session, we measured the mass of each spider using an analytic scale (Kern-PCB 250-3). None of the individuals molted over the course of the experiment. At the end of the study, we also measured the prosoma width of the preserved specimens with 0.04 mm accuracy using an ocular micrometer calibrated with a stage micrometer. *Carrhotus xanthogramma* overwinters mostly as a penultimate or antepenultimate (i.e., last instars right before the adult stage). Thus, in autumn, it can be collected at a relatively uniform ontogenetic stage (Markó and Keresztes 2014). Within the genus *Carrhotus*, only *C. xanthogramma* occurs in Europe (Nentwig et al. 2021), thus, immatures could not be confused with other species. However, to check the taxonomic identity of the individuals, we kept alive 10 randomly selected spiders (5 females and 5 males) and fed them with *D. hydei* until their final molts. Finally, we preserved the raised and immature individuals in 70% ethanol, and using a binocular stereomicroscope (Leica MZ6), we confirmed their taxonomic identity after Nentwig et al. (2021). We determined the sex of each immature (penultimate or antepenultimate) spider after the following criteria—specimens with a slightly enlarged palpal tarsus were considered as males, while specimens with a pre-epigyne (undeveloped, thus, just visible external genitalia of the females) but no enlarged palpal tarsus were considered as being females. We excluded the data of the 2 specimens (1 from Site_Cs and 1 from Site_M1) that did not have either enlarged palpal tarsus or pre-epigyne (i.e., earlier instars) from our analyses. In accordance with the findings of Markó and Keresztes (2014), we found that most of the population (60%) was female.

Behavioral assays

We assessed activity, risk-taking, and prey capture behavior for each spider individual on 3 consecutive days and repeated these assays weekly for 4 weeks in the same order. We performed our assays between 0900 and 1600 h (as that was the most active period for these animals) based on the model species' circadian activity (Mezőfi et al. 2019). We recorded the assays using recording platforms (Kaiser RS 10 copy stands) equipped with a camera (Panasonic HC-X920 HD), which permitted the recording of the behavioral traits of several individuals simultaneously. During the assays, we also continuously recorded the temperature. To minimize human disturbance, only one person remained in the behavioral laboratory to manipulate the spiders, handle the cameras, and check the assays. During the experimental series, we measured each individual's different behaviors in the same Petri dish to avoid generating unwanted random noise in a novel environment.

Measuring activity

First, we positioned the trays holding the Petri dishes with spiders on the copy stands. After that, we waited 5 min before we started recording the activity of the spiders. For spiders, the Petri dishes represented the environment in which we measured their activity. The activity was recorded on every experimental day for 30 min. Later, we analyzed the recordings using the software ToxTrac version 2.84 (Rodriguez et al. 2018) to calculate the 'Activity rate', that is, the total time of the spiders was engaged in locomotion divided by the assay's length.

Measuring risk-taking behavior

We positioned the plastic trays containing the spiders on the copy stands and waited 5 min before starting. Thereafter, to expose the spiders to a physical stimulus that they may perceive as a potential threat, we gently lifted the plastic tray 5 cm high and dropped it back on the copy stand. To test the short-term plasticity of risk-taking behavior, we repeated this process 10 min later, that is, we tested the risk taking of the spiders twice (2 intra-assay trials) in one assay. Ten minutes after the second "startling" process, we stopped recording the behavior of spiders.

We calculated the "Freezing duration" in seconds as the time between receiving the startling stimulus and the moment when the spiders started moving again after freezing. The tested individuals demonstrated 3 types of behavioral responses to the stimulus. First, spiders froze immediately after receiving the stimulus (majority, 91.6% of all cases); second, before freezing, they ran about for a short time (≤ 1 s) (minority, 6.4%), while the third continued their activity without demonstrating any clear response to the stimulus (rare, 2%). We omitted the time of running for the individuals who ran before freezing as it was negligible compared to these individuals' total time of freezing. Individuals that did not respond to the stimulus by freezing received a zero value (seconds), and individuals without any movement in the first or second intra-assay trial, received a value of 601 (seconds) for the corresponding trial. An individual with a low Freezing duration was considered risk tolerant (i.e., a bold one), while the one with a high Freezing duration score was considered risk averse (i.e., a shy one).

Measuring prey capture latency

For testing the spiders' willingness to attack, we gently tipped over the top of the Petri dishes, and using featherweight entomology forceps, we inserted 3 flightless *D. hydei* in the dishes quickly. After that, we immediately placed the dish on the copy stand under the camera and recorded the spiders' hunting. We continuously fed the spiders on a particular plastic tray by the previous method and placed them under the camera in the same order as they were on the tray. The whole process was recorded, and after placing the last spider under the camera, we recorded their activity for further 30 min. We checked the Petri dishes 24 h later, counted the number of live fruit flies, and removed both the living and the dead ones.

The same observer assessed all the video recordings and noted the exact time when the spiders were placed under the camera and when each spider successfully caught the first, the second, and the third fruit fly. Then, we calculated the capture latency (i.e., the time in seconds between the placement of the spider under the camera and the capture of the prey) for each of the flies that were captured within the first 30 min.

Individuals catching their prey just when the prey was offered received a value of 1, 2, and 3 (seconds), and individuals who caught the prey later than 30 min of observation but within 24 h scored as 1,801, 1,802, and 1,803 s for catching the first, second, and third fruit fly, respectively. However, most spiders caught the first prey very early, and many spiders caught the third fly later than 30 min. Thus, we computed the arithmetic mean of the capture of the first, second, and third prey (hereinafter "Capture latency") to characterize the spiders' willingness to attack. In 3 cases, the spiders did not catch the third fly at all, thus, these observations were excluded from the analyses.

Statistical analyses

All statistical analyses were performed within the R (v.3.5.3.) statistical environment (https://www.R-project.org/). All the analyzed data with their R script are provided in the files entitled "Supplementary data" and "Supplementary codes," respectively. To find out which predictors explain a significant amount of variance in the behavior of the spiders used in our study, we built various linear (nonmixed and mixed) models (described in more detail below) using the "lme4" R package (https://CRAN.R-project.org/package=lme4). To statistically control the unwanted effect of the temperature, first, we built Linear Models (LMs) where the behavioral traits were the response variables, and the temperature was the predictor. In the case of Freezing durations, we used log transformation to approach a normal distribution. After transformation, although the Freezing duration was right-censored (601 s; see above), diagnostic statistics did not indicate a noticeable deviation from the assumptions of linear models. In our further models, we used the residuals of the abovementioned LMs as response variables.

Analyzing the body parameters

First, we calculated a set of new variables, which made it possible to analyze the variation in body parameters of spiders properly. "Mean mass" was the arithmetic mean of the mass (in mg) of the spiders measured at the beginning ("Initial mass") and the end ("Final mass") of the experiment. We computed the "Relative mass change" as follows: (*Final mass – Initial mass*)/ *Initial mass* × 100. To estimate the "Body condition" of the individuals, we used the residuals of the regression of (log) Mean mass on (log) Prosoma width (Jakob et al. 1996).

Using LMs, we ran separate analyses with Initial mass, Relative mass change, Prosoma width, and Body condition as response variables, while the Site, Sex, and their interaction were entered as predictor variables. In Relative mass change, we used log transformation [$log(Relative\ mass\ change + 100)$] to approach the normal distribution.

Analyzing the behavioral mean and the relationship with the body parameters

To test what affects the behavioral means, we ran various linear mixed-effects models (LMMs), separately, in which the given behavioral variable was entered as a response variable into the model. The initial LMMs comprised the Site, Session number, and Sex as predictor variables and the specific ID numbers as a random factor. In the Freezing duration, the model also comprised the Trial number (intra-assay trials, a 2-level factor) as a predictor variable. The R syntaxes of the initial (both sex included) models were as follows:

lmer(*Activity rate res. ~ Site + Session nr. + Sex + (1|Spider. ID)*), *lmer*(*Freezing duration res. ~ Site + Session nr. + Sex + Trial nr. + (1|Spider.ID)*), and *lmer*(*Capture latency res. ~ Site + Session nr. + Sex + (1|Spider.ID)*).

Preliminary results showed that Sex interfered with specific body parameters and behavioral mean (see the Results). So, we analyzed the behavioral data of females and males separately. Furthermore, we entered 2 new predictor variables, Body condition and Prosoma width, into the sex-specific mixed models. For model summaries, see the Supplementary Material.

LMMs are powerful tools for analyzing complex datasets, for example, in behavioral ecology or evolution, since model estimates are usually robust to violations of distributional assumptions (Schielzeth et al. 2020). Nevertheless, before interpreting the model outcomes, we performed numerous model diagnostic statistics to avoid misleading results based on statistical artifacts. Following the recommendations of Garamszegi et al. (2014), we checked the assumptions about the distribution of residuals (normality and homogeneity), and we calculated variance inflation factors (VIF) to examine the issues about multicollinearity. In the case of LMs, based on our models, we computed the η^2 values (with 90% CIs due to the one-tailed tests) for our predictors using the R packages "sjstats" (https://CRAN.R-project.org/package=sjstats) and "MBESS" (https://CRAN.R-project.org/package=MBESS). Regarding the LMMs, following the procedure of Garamszegi et al. (2014), we estimated the statistical significance of the focal predictors using the likelihood ratio tests (full models versus restricted models without the given predictor), where the significance was described by the probability function of the chi-square distribution (at df = 1). Finally, we calculated the effect sizes (Cramer's V) with 95% CIs for each focal relationship (Garamszegi et al. 2014).

Calculating behavioral repeatability and estimating behavioral syndrome structure

As every spider was tested 4 times, we calculated their behavior's repeatability (as a proxy of interindividual consistency) and evaluated the correlational relationships between the measured behavioral trait variables. For calculating these estimates, we ran multivariate Markov Chain Monte Carlo Generalized Linear Mixed Models (MCMCglmms) for females and males separately, using the Bayesian "MCMCglmm" R package (Hadfield 2010). In these multivariate models, our mean-centered behavioral variables (Activity rate, Freezing duration in the first and second trials, and Capture latency) were (together) the response variables, while specific IDs were coded as random effect. In order to statistically control the putative effect of temporal repetition, we entered the Session number as a predictor variable (as a covariate) into the models. Applying such a model structure was necessary because (consistency) repeatability estimates were calculated (after Nakagawa and Schielzeth 2010) using the variance components obtained from these models, and ignoring time-related change might lead to biased estimates of repeatability (Biro and Stamps 2015). Following the approach of Dingemanse and Dochtermann (2013), we used these multivariate models to decompose phenotypic (co) variances into inter- and intraindividual components and, as Dingemanse and Dochtermann (2013) recommended, we used only the interindividual (co)variance components to evaluate the relationship between each measured behavioral

trait variable (i.e., between-individual correlations were calculated). In these models, we set the intraindividual covariance to 0 since the different behavioral traits were not tested at the same time (Dingemanse and Dochtermann 2013). We used a weakly informative inverse gamma prior and specified our MCMCglmms with 1 300 000 iterations, 300 000 iterations "burn-in" and a thinning interval of 1,000. Both for the repeatability estimates and the correlation coefficients (effect sizes), 95% credible intervals were calculated based on the posterior mode of their estimates. In order to evaluate the (dis)similarity of the behavioral syndrome structure of the sexes, we performed Mantel's test on the sex-specific matrices of the posterior correlation coefficients using the "mantel" function of the R package "ecodist" (https://CRAN.R-project.org/package=ecodist). Following the methods of Royauté et al. (2015), we calculated Δr, the average difference in pairwise correlations between sexes, and, as Royauté et al. (2015), Δr values are interpreted based on the following scale: $0 < |\Delta r| < 0.2$, no to low effect; $0.2 < |\Delta r| < 0.5$, medium effect; $0.5 < |\Delta r|$, strong effect. Regarding the behavioral correlations with the highest $|\Delta r|$, we illustrate these relationships using the posterior modes of our random effects (i.e., best linear unbiased predictors—BLUPs) from our multivariate models after Houslay and Wilson (2017). Finally, we determined statistical support for covariances (correlations) by differences in deviance information criteria (DIC) values. Thus, as Dingemanse and Dochtermann (2013) proposed, we compared the DIC of constrained (inter- and intraindividual covariances were set to 0) and unconstrained models (only intraindividual covariance was set to 0) for a better fit. Significant behavioral correlations (based on nonoverlap of the CI with 0) were accepted when 5< DIC constrained – DIC unconstrained (Kralj-Fišer et al. 2017). For model summaries and detailed results, see the Supplementary Material.

Analyzing the intraindividual behavioral variability

As the behavioral trait variables were measured multiple times, we computed the residual individual standard deviation (riSD) as a proxy of IIV. IIV values refer to behavioral predictability in the following way: The higher the value of IIV, the lower the behavioral predictability. Therefore, we calculated the riSD values after the procedure proposed by Stamps et al. (2012). First, we fitted LMMs in which we incorporated a temporal reaction norm. In these models, the response variable was the given behavioral trait variable, the fixed effect was the Session number (i.e., time, altogether 4 sessions), and the random effects were represented by Session number as a random slope and by specific ID as a random intercept (R syntax: *lmer*(*Behavioural trait res. ~ Session nr. + (Session nr.|Spider.ID)*)). Then we extracted the residuals of the models and computed the riSD index values. Finally, we entered the riSD values (as response variables) into LMs where the predictor variables were represented by the Site, Sex, and their interaction.

Results

Variability in body parameters

Based on the η^2 values, the largest amount of variance was accounted for by Sex concerning the Initial mass (21.8 %) and Prosoma width (16.4 %); that is, immature females had lower mass and a narrower prosoma than immature males in *C. xanthogramma* (Table 1 and Figure 1). We also found

sex-specific variance in the Relative mass change of the immature spiders. The body mass changed differently, as females gained (mean ± SD: 6.67 ± 16.08 %; N = 53) while males maintained or slightly lost (mean ± SD: –0.75 ± 12.64 %; N = 36) body mass during the study (Table 1 and Figure 1). Generally, larger individuals lost while smaller ones gained mass; thus, Initial mass negatively correlated with Relative mass change (Pearson's $r = –0.64$; $P < 0.001$). Furthermore, we detected interpopulation variation in the Initial mass and Body condition but not in the other body parameters of the immature individuals (Table 1 and Supplementary Figure S1).

Variability in behavior

Robust sex-specific differences were detected in *C. xanthogramma* regarding the Activity rate and Freezing duration (Table 2). Males were more active and took a higher risk (shorter Freezing duration) toward a potentially threatening abiotic stimulus than the females (Figure 2).

Furthermore, in contrast with the females, males' activity increased with time, and the corresponding effect size and the associated CIs indicated medium to strong effects (Table 2 and Supplementary Figure S2). Regarding the Freezing duration, though both females and males reacted more sensitively (small to strong effect) to the second intra-assay startling stimuli (Figure 2), in the long term, only the females reacted to the threatening abiotic stimuli more and more sensitively (strong effect, the Freezing duration increased with time), while males did not show such pattern (Table 2 and Supplementary Figure S2). Finally, male individuals tended to catch the offered prey faster with the increasing number of test sessions (marginal relationship with a small to strong effect, the Capture latency decreased with time) (Table 2 and Supplementary Figure S2).

We detected a marginally significant positive relationship (with a small effect) between the Prosoma width and the Activity rate in males but not in females (Table 2 and Figure 3). We found in both sexes that Freezing duration was related positively (small to strong effect) to the Body condition and related negatively (only marginally with a small to medium effect) to the Prosoma width, in both cases with a stronger effect in males than females (Table 2 and Figure 3). A significant negative relationship (with a small to strong effect) was found between the Capture latency and Prosoma width in males, that is, larger individuals tended to catch the prey faster (Table 2 and Figure 3). No such relationship was found in females (Table 2 and Figure 3). Finally, our analyses revealed a small to strong effect of the collecting site on the Freezing duration (regarding females and males) and the Capture latency (regarding only females) (Table 2 and Supplementary Figure S3).

Behavioral repeatability, correlation structure, and IIV

Both females and males showed behavioral repeatability regarding all of the measured behavioral traits (Activity rate, Freezing duration in the first and second trials, and Capture latency) (Table 3). In females, we found evidence for a behavioral syndrome involving all measured behavioral traits: Activity rate was negatively associated with Freezing duration (a measure of risk taking) and with Capture latency, while a positive relationship was found between the latter 2 behavioral traits (Figure 4). In males, we found a significant (negative) correlation only between the Activity rate and Freezing duration (measured in the

Table 1. Site- and sex-specific differences in body parameters in *Carrhotus xanthogramma* immatures ($N = 90$).

Response variable	Predictors	df	Sum of Sq.	Mean of Sq.	F-value	P-value	Effect size (η^2)*	CI_{lower}	CI_{upper}
Initial mass (mg)	Site	2	286.54	143.27	3.491	0.035	0.059	0.003	0.166
	Sex	1	1,050.31	1,050.31	25.591	**<0.001**	**0.218**	**0.111**	**0.350**
	Site:Sex	2	42.02	21.01	0.512	0.601	0.009	NA	0.058
	Residuals	84	3,447.50	41.04	NA	NA	NA	NA	NA
Relative mass change	Site	2	0.08	0.04	2.299	0.107	0.050	NA	0.133
	Sex	1	0.09	0.09	5.046	**0.027**	**0.054**	**0.003**	**0.152**
	Site:Sex	2	0.00	0.00	0.010	0.990	0.000	NA	NA
	Residuals	83	1.47	0.02	NA	NA	NA	NA	NA
Prosoma width (mm)	Site	2	0.32	0.16	2.979	0.056	0.055	NA	0.152
	Sex	1	0.95	0.95	17.766	**<0.001**	**0.164**	**0.066**	**0.290**
	Site:Sex	2	0.03	0.02	0.272	0.762	0.005	NA	0.040
	Residuals	84	4.50	0.05	NA	NA	NA	NA	NA
Body condition	Site	2	0.41	0.21	6.179	**0.003**	**0.123**	**0.028**	**0.230**
	Sex	1	0.05	0.05	1.358	0.247	0.014	NA	0.084
	Site:Sex	2	0.10	0.05	1.433	0.244	0.028	NA	0.101
	Residuals	84	2.81	0.03	NA	NA	NA	NA	NA

Note: Effect size values are bolded if the related CI does not overlap with zero.
*Small effect: $0.02 \leq \eta^2 < 0.13$; Medium effect: $0.13 \leq \eta^2 < 0.26$; Large effect: $0.26 \leq \eta^2$.
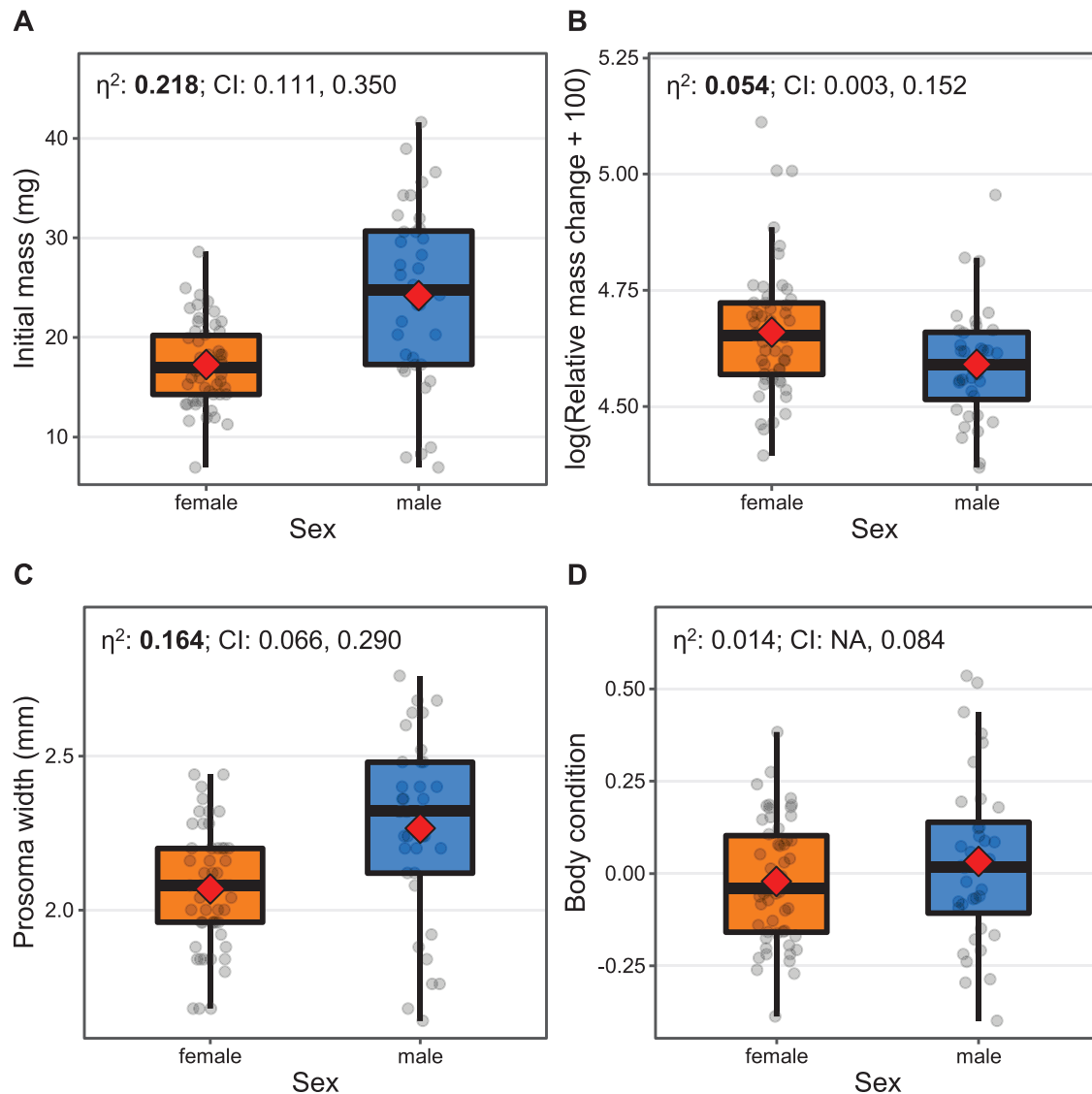
Figure 1. Sexual differences in body parameters (A—Initial mass; B—Relative mass change; C—Prosoma width; D—Body condition) in *Carrhotus xanthogramma* immatures. The distance between the box bottom (first quartile) and top (third quartile) corresponds to the interquartile, while the whisker shows the nonoutlier range. The red diamond and the bold horizontal line indicate the mean and median values, respectively. Data points were jittered horizontally. Effect size (η²) and related 90% CI are displayed on the corresponding panel. Effect size values are bolded if CI does not overlap with zero.

second trial) (Figure 4). Based on the differences in DIC values (female ΔDIC = 30.844; male ΔDIC = 9.945), the unconstrained models were substantially more well supported by the data than the models in which the interindividual covariances were set to 0 (Table 3), thus significant correlations were accepted. However, the Mantel test did not provide clear evidence for sex-specific behavioral syndromes (Figure 4) as a marginally significant overall correlation (Mantel test 1 000 000 permutations: $r = 0.924$; $P = 0.084$) was found between the behavioral correlation matrices. Nevertheless, the highest sex-related differences in correlation estimates (Δr) were found in the following behavioral trait combinations: Activity rate versus Capture latency (Δr = 0.300) and Freezing duration (measured in the second trial) versus Capture latency (Δr = −0.247) (Table 3 and Figure 5). None of the predictors (Site, Sex, and their interaction) had an effect on IIV (i.e., behavioral predictability) (Table 4).

Discussion

We tested for sex-specific differences in the essential fitness-related traits and their correlation structure in *C. xanthogramma* immatures. In general, we found sex-specific differences in specific body parameters and behavioral traits between females and males before reaching their reproductive stage, suggesting different life-history strategies.

Testing the sexual dimorphism in specific body parameters, we found that the immature *C. xanthogramma* males had a wider prosoma and greater initial body mass than the female conspecifics (Figure 1). Our results contrasted with the general pattern among spiders regarding their body size because adult spider males are often smaller than females (Head 1995). Though a few exceptions with a reversed pattern exist, for example, in salticids (Prenter et al. 1999; Lim and Li 2004), the adult males of the species studied here are also smaller than the adult female conspecifics (Kim and Lee 2014). One possible explanation for our findings could be

Table 2. Results from linear mixed models, in which the behavioral traits of *Carrhotus xanthogramma* immatures ($N = 90$) were the response variables.

Response variable	Model	Predictors	Likelihood Chi²	$P_{Likelihood\ ratio}$	Effect size (Cramer's V)*	CI$_{lower}$	CI$_{upper}$
Activity rate	Both sex included	Site	1.087	0.581	0.110	−0.100	0.310
		Sex	8.259	0.004	0.303	0.102	0.480
		Session nr.	7.723	0.006	0.293	0.091	0.471
	Only females	Site	0.198	0.906	0.061	−0.211	0.323
		Session nr.	0.500	0.480	0.096	−0.176	0.355
		Body condition	0.666	0.415	0.111	−0.162	0.368
		Prosoma width	0.216	0.642	0.063	−0.208	0.326
	Only males	Site	2.634	0.268	0.271	−0.064	0.550
		Session nr.	12.110	<0.001	0.580	0.311	0.763
		Body condition	0.297	0.586	0.091	−0.245	0.407
		Prosoma width	3.148	0.076	0.296	−0.036	0.569
Freezing duration	Both sex included	Site	9.604	0.008	0.327	0.128	0.500
		Sex	7.067	0.008	0.280	0.078	0.461
		Session nr.	26.869	<0.001	0.546	0.383	0.677
		Trial nr.	16.234	<0.001	0.425	0.239	0.581
	Only females	Site	6.303	0.043	0.342	0.081	0.558
		Session nr.	44.182	<0.001	0.905	0.840	0.944
		Trial nr.	7.592	0.006	0.375	0.119	0.584
		Body condition	6.599	0.010	0.350	0.090	0.565
		Prosoma width	2.720	0.099	0.225	−0.046	0.464
	Only males	Site	14.689	<0.001	0.639	0.393	0.800
		Session nr.	0.000	0.995	0.001	−0.328	0.330
		Trial nr.	9.617	0.002	0.517	0.227	0.723
		Body condition	10.311	0.001	0.535	0.251	0.735
		Prosoma width	3.504	0.061	0.312	−0.018	0.581

Table 2. Continued

| Response variable	Model	Predictors	Likelihood Chi²	$P_{\text{Likelihood ratio}}$	Effect size (Cramer's V)*	CI$_{\text{lower}}$	CI$_{\text{upper}}$
Capture latency	Both sex included	Site	8.650	**0.013**	**0.310**	0.110	**0.486**
		Sex	2.335	0.126	0.161	-0.048	0.356
		Session nr.	1.091	0.296	0.110	-0.099	0.310
	Only females	Site	4.370	0.112	**0.284**	0.018	**0.513**
		Session nr.	0.029	0.864	0.023	-0.246	0.289
		Body condition	0.937	0.333	0.132	-0.141	0.386
		Prosoma width	0.388	0.533	0.085	-0.187	0.345
	Only males	Site	3.355	0.187	0.305	-0.026	0.576
		Session nr.	3.335	0.068	0.304	-0.027	0.575
		Body condition	0.066	0.798	0.043	-0.290	0.366
		Prosoma width	7.976	**0.005**	**0.471**	0.168	**0.692**

Note: Significance levels (*P*) and effect sizes (Cramer's V) originated from the corresponding likelihood ratio test that compared the model fit of the full model and the reduced model after excluding the given predictor. The 95% CIs around effect sizes originated from the parametric bootstrap performed on data simulated according to the model's predictions. Effect size values are bolded if the related CI does not overlap with zero.

*Small effect: $0.1 \leq V < 0.3$; Medium effect: $0.3 \leq V < 0.5$; Large effect: $0.5 \leq V$.

that the female sample collected in autumn comprised proportionally more antepenultimate individuals than the male population. A previous study (Markó and Keresztes 2014) detected a sex-biased temporal asynchrony in the population structure of *C. xanthogramma*, implying differential timing of maturity. It was observed that adult males were more numerous in April while females in May (Markó and Keresztes 2014), suggesting that adult males reached adulthood and became ready for reproduction earlier than females (i.e., *C. xanthogramma* shows protandry), which mating strategy could result in female-biased sexual size dimorphism (smaller males relative to females) in spiders (Maklakov et al. 2004). Also, in our reared individuals, the mean developmental time (calculating from the time of collection, mean ± SD, in days) was shorter in males than females (56.2 ± 8.93; $N = 5$ vs. 102.4 ± 27.57; $N = 5$).

It seems that body parameters concerned are subject to opposing evolutionary forces. On one hand, selection acts for protandry, that is, rapidly developing males (with a decreased male size) have higher fitness, especially in web-builder spiders (Head 1995). But on the other hand, a larger size may also increase male fitness as a heavier male is usually more successful than a smaller one in a direct competitive context (Kasumovic and Andrade 2009; Kasumovic et al. 2011). Our results (Figure 1) might be explained by the fact that the primary objective of adult males is to find a mate for copulation as soon as possible, thus they often do not feed at all or only occasionally (Givens 1978; Foelix 2011). Therefore, accumulating additional nutrient reserves (i.e., greater body mass) before maturity might provide them with an adaptive advantage. Furthermore, mating success is often associated with male size (Sivalinghem et al. 2010; Golobinek et al. 2021), and for example, in another jumping spider *Phidippus clarus*, heavier males were more successful in intraspecific male–male competition (Elias et al. 2008). As sex-specific selection forces favor males with larger body size (Fernández-Montraveta and Moya-Laraño 2007), to maximize their fitness outputs, accumulating nutrient reserves before maturity could be crucial for males. In contrast, females with a relatively longer lifespan than males may, over the longer adulthood, compensate for their slower rate of weight gain during immaturity. This temporal asynchrony in growth patterns between females and males could be sourced by the differential reproductive investment, affecting behavioral and feeding patterns.

Consistent individual differences in behavior are linked with consistent individual differences in energy metabolism (Biro and Stamps 2010; Holtmann et al. 2017a). In our study, males were more active and bolder than females (Table 2 and Figure 2), which may be explained by the different physiological backgrounds of the sexes. Spider males usually show higher metabolic rates than females (Schmitz 2004; Walker and Irwin 2006; but see Kotiaho 1998). Higher level of metabolic activity often associates with a shorter lifespan (Réale et al. 2010; Kralj-Fišer and Schuett 2014). Similarly to our results, Chapman et al. (2013) found that rock pool prawn (*Palaemon elegans*, Palaemonidae) males were more active and bolder than the females, which usually live for twice as long as males. Field observations of Markó and Keresztes (2014) implied that *C. xanthogramma* males mature earlier and have a shorter lifespan than females. These results suggest that immature males' higher activity and boldness stem partly from their assumed higher rate of metabolism.
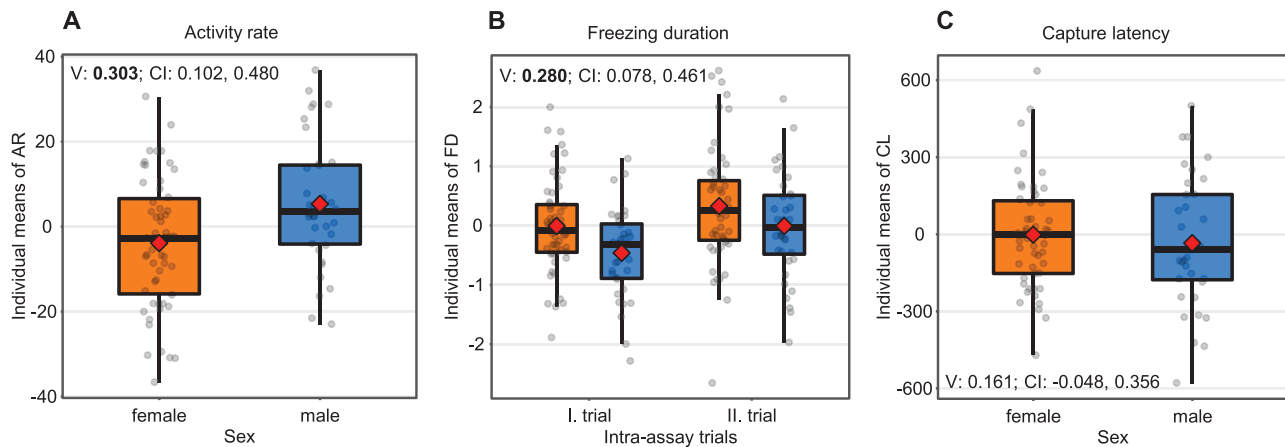
Figure 2. Sexual differences in behavioural traits (A—Activity rate; B—Freezing duration; C—Capture latency) of *Carrhotus xanthogramma* immatures. The distance between the box bottom (first quartile) and top (third quartile) corresponds to the interquartile, while the whisker shows the nonoutlier range. The red diamond and the bold horizontal line indicate mean and median values, respectively. Data points were jittered horizontally. Effect size (Cramer's V) and related 95% CI are displayed on the corresponding panel. Effect size values are bolded if CI does not overlap with zero. AR, Activity rate; FD, Freezing duration; CL, Capture latency.

In this study, immature *C. xanthogramma* males showed higher activity than immature females, which results were in contrast with a previous study, reporting that the adult males were less active than adult females (Mezőfi et al. 2019). One possible explanation for this pattern might be that the *C. xanthogramma* individuals change their strategy with maturation: Immature males forage much more intensively and accumulate nutrient reserves, while immature females, to protect their condition, remain more cautious and less active. In contrast, mature males feed only occasionally and use up their nutrient reserves, while mature females feed actively to gain more and more energy to increase their egg production. Ontogenic behavioral shift was observed, for example, in the Sydney funnel-web spider (*Atrax robustus*, Atracidae), where adult females reacted more intensively to an aversive stimulus than the juveniles (Duran et al. 2022). Furthermore, behavioral changes were also documented among ontogenetic stages in other arthropod taxa, suggesting that individuals could respond flexibly according to their current physiological requirements (e.g., Gyuris et al. 2012; Niemelä et al. 2012; Kralj-Fišer and Schuett 2014).

In males, both the activity and the willingness to attack a prey increased (but the latter was only marginally) with the repeated test sessions (Table 2 and Supplementary Figure S2). We observed that males did not gain body weight in the course of this study. This was probably because the feeding regime (3 *Drosophila*/week) followed did not meet the males' (possibly higher) nutritional needs (see Figure 1). Hunger can increase activity (Walker et al. 1999), and activity is closely linked with the metabolic rate (Schmitz 2004; Walker and Irwin 2006). Thus, the physiological differences and environmental conditions could be responsible for the males' increased activity and the willingness to attack modulated by the individuals' current hunger level. A self-excitation process could be generated in males due to the strong link between physiology and behavior. Their assumed higher (base) metabolic rate (see previously) would result in a higher level of hunger and induce a higher level of activity to find prey, which would further increase the metabolic rate and generate other physiological and behavioral consequences.

A prior negative experience can reduce the degree of boldness (Frost et al. 2007). Therefore, accordingly, both females and males increased their latency to movement initiation in the risk-taking assay (in the short term, see Table 2 and Figure 2). However, in contrast to males, the Freezing duration of females was also significantly increased with the number of test sessions (Table 2 and Supplementary Figure S2). A similar (but insignificant) trend was also observed in *Philodromus albidus* (Philodromidae) females (Michalko et al. 2017), which could be considered as an effect of sensitization to a threatening stimulus (Blumstein 2016), causing the manifestation of a risk-averse behavior among females.

Several studies (e.g., Royauté et al. 2014; Ingle et al. 2018; Michalko and Řežucha 2018) have shown a relationship between body parameters and behavior. We also found a significant relationship between Freezing duration and condition both in females and males—individuals in better condition tended to be more risk averse (i.e., showing longer Freezing duration) (Table 2 and Figure 3). These results support the "asset-protection principle," which proposes that an individual with a better body condition should be more risk averse than an individual with a poorer body condition (Clark 1994; Kralj-Fišer and Schuett 2014; Moran et al. 2021). Royauté et al. (2014) also observed decreasing boldness with increasing body condition in the jumping spider, *E. militaris*, although the direction of the relationship between boldness and condition may depend on the actual experimental or ecological context (Johnson and Sih 2007). Besides this, the response to a threatening stimulus could be based mainly on some individual-specific traits, such as body size and sex (i.e., being male or having a larger body size could initiate a bolder response) (Table 2; Figure 3). Regarding Capture latency, the negative relationship between behavior and body size could play an essential role in the hunting decisions but only in males (Table 2; Figure 3).

In this study, an interpopulation variation was detected for fitness-related traits such as Initial mass, Body condition, Freezing duration, and Capture latency (Tables 1 and 2; Supplementary Figures S1 and S3). Supporting our results, Michalko and Dvoryankina (2019) recently communicated that certain traits of another spider species could vary along
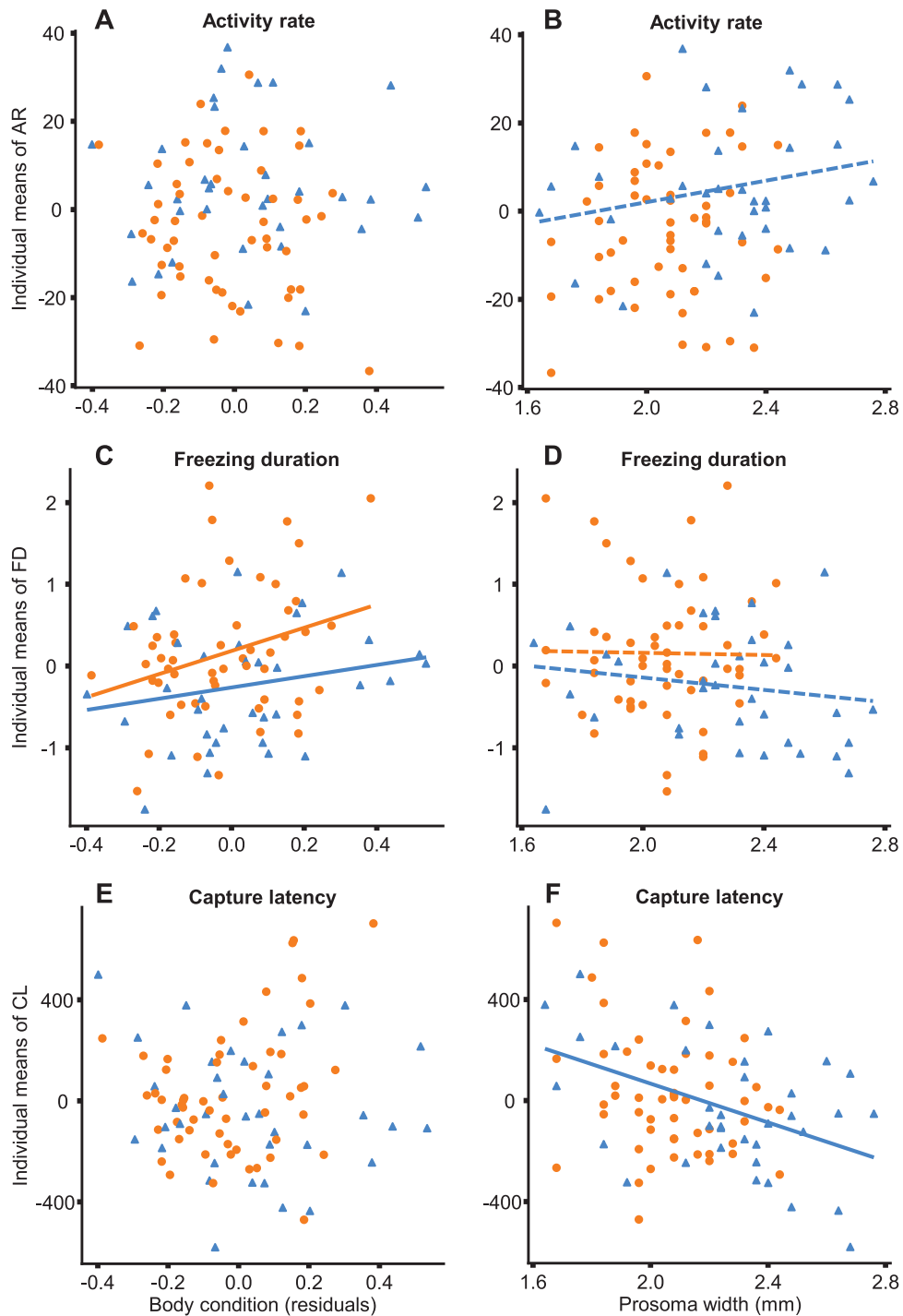
Figure 3. The linear relationship between a tested behavioral trait and body parameters such as the Body condition (A, C, E) and Prosoma width (B, D, F) in female and male *Carrhotus xanthogramma* immature individuals. Solid lines indicate significant ($P_{\text{Likelihood ratio}} < 0.05$; effect size CI excludes 0) relationships, while dashed lines indicate marginally significant ($P_{\text{Likelihood ratio}}$ between 0.05 and 0.1) relationships. AR, Activity rate; FD, Freezing duration; CL, Capture latency. Colors represent the sexes (orange—female, blue—male).

a spatial gradient even within a single orchard. Individuals from the orchard centers can be larger than those from the edges. Developmental diet quality can affect the condition (Taylor et al. 2011) and, according to the meta-analysis by Moran et al. (2021), a low-quality diet increases boldness in several ecological contexts. Thus, the differences in the qualitative or quantitative composition of the arboreal arthropod (potential prey) assemblages of the different sampling sites

could explain the detected interpopulation variations. Besides this, personality-matching habitat choice (Holtmann et al. 2017b) cannot be excluded.

Sex-related differences in repeatability, behavioral correlations, IIV, and their mechanistic background have not been adequately studied in the invertebrate literature. Therefore, more studies are needed to fill these gaps in knowledge. Here, the tested behavioral traits showed moderate repeatability

Table 3. Results of multivariate MCMCglmms testing for interindividual correlations (estimate with 95% CIs) of the measured behavioral traits (AR, Activity rate; FD_I and FD_II, Freezing duration in the first and second trial; CL, Capture latency) in *Carrhotus xanthogramma* immatures by sex.

	Females			
	Unconstrained model DIC 2242.34			
	Constrained model DIC 2273.184			
	AR	FD_I	FD_II	CL
AR	**0.370 (0.244; 0.512)**			
FD_I	**−0.621 (−0.815; −0.219)**	**0.226 (0.143; 0.381)**		
FD_II	**−0.622 (−0.808; −0.269)**	**0.664 (0.423; 0.858)**	**0.360 (0.224; 0.475)**	
CL	**−0.501 (−0.703; −0.060)**	**0.407 (0.036; 0.705)**	**0.555 (0.096; 0.748)**	**0.310 (0.202; 0.481)**
	Males			
	Unconstrained model DIC 1508.846			
	Constrained model DIC 1518.791			
	AR	FD_I	FD_II	CL
AR	**0.337 (0.207; 0.519)**			
FD_I	−0.376 (−0.749; 0.027)	**0.232 (0.128; 0.419)**		
FD_II	**−0.412 (−0.773; −0.044)**	**0.528 (0.071; 0.801)**	**0.294 (0.157; 0.458)**	
CL	0.048 (−0.525; 0.359)	0.451 (−0.011; 0.765)	0.299 (−0.255; 0.654)	**0.385 (0.201; 0.528)**
	Δr (male r − female r)			
	AR	FD_I	FD_II	CL
AR				
FD_I	−0.012			
FD_II	0.141	−0.072		
CL	**0.300**	0.112	−0.247	

Note: Repeatability estimates (with 95% CIs) of each behavioral trait were shown in the diagonals. Δr represents the average effect size of the difference in correlation coefficients between sexes. Unconstrained (covariance within individuals was set to 0) and constrained models (covariances between and within individuals were set to 0) were compared. Correlations and repeatability estimates were calculated from the unconstrained models and significant correlations (based on nonoverlap of the CI with 0) were accepted when $5<$ DIC constrained − DIC unconstrained. Significant correlations and repeatability estimates are bolded. $|\Delta r|$ values >0.2 are indicated in bold. For model summaries and detailed results, see the Supplementary Material.
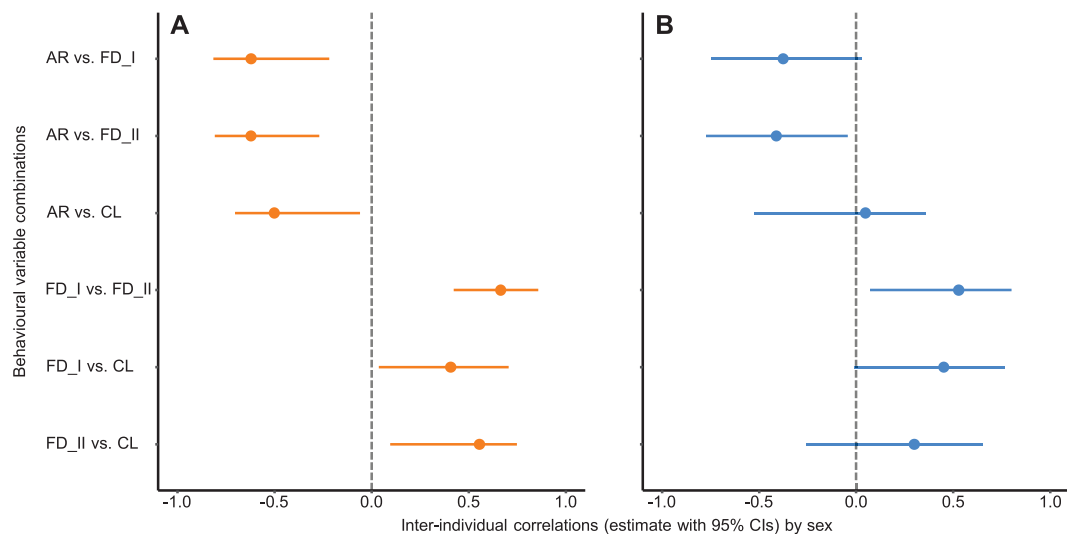
Figure 4. The correlation structure (A—female; B—male) of the measured behavioral traits in *Carrhotus xanthogramma* immatures. Results of multivariate MCMCglmms testing for interindividual correlations. AR, Activity rate; FD_I and FD_II, Freezing duration in the first and second trial; CL, Capture latency.
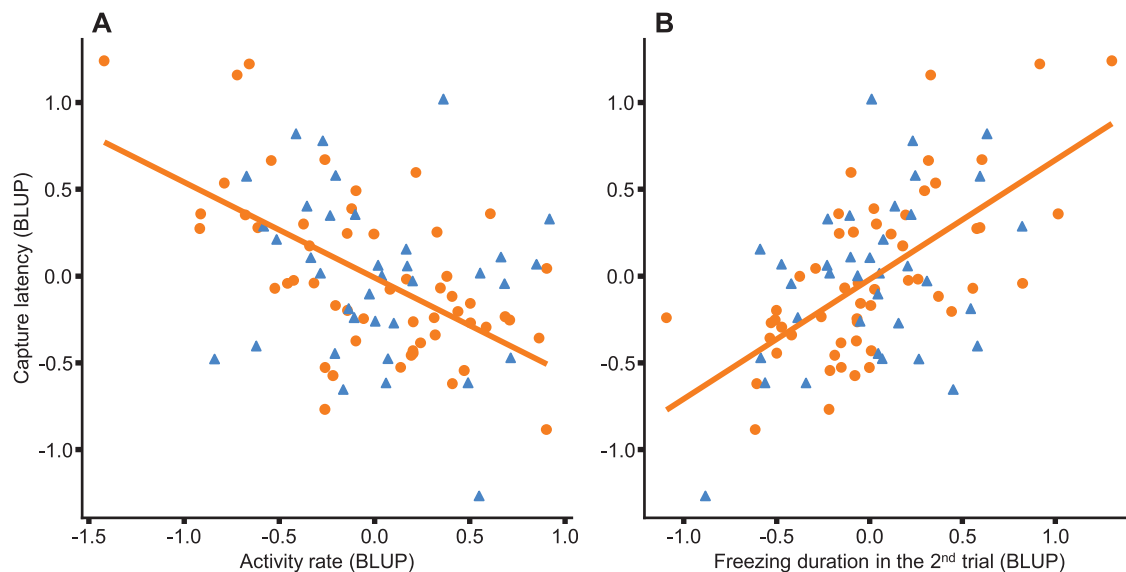
Figure 5. Sexual differences in interindividual behavioral correlations (A—Activity rate vs. Capture latency; B—Freezing duration in the second trial vs. Capture latency). Plots represent linear relationships between behavioral traits with highest difference in correlation estimates between sexes (Δr, see Table 3.). Values (best linear unbiased predictors—BLUPs) were extracted from multivariate MCMCglmms using the posterior modes of random effects (specific IDs). Solid lines indicate significant (effect size CI excludes 0) relationships. Colors represent the sexes (orange—female, blue—male). Note the absence of significant relationships between behavioral traits in males.

in both sexes (Table 3), reflecting consistent interindividual behavioral differences, which findings fit the concept of animal personality (Réale and Dingemanse 2012). A meta-analytic study (Bell et al. 2009) found that among invertebrates, the behavior of females is more repeatable than that of conspecific males. However, the direction of the sex differences in repeatability may depend on the specific behavior being considered (Bell et al. 2009). In the present study, sex-specific differences were not found concerning the repeatability estimates as their credible intervals were overlapped (Table 3).

Sex-specific behavioral syndromes were reported in certain invertebrate taxa, for example, in field crickets (*Gryllus integer*, Gryllidae), and it seems that these syndromes were partially driven by genetics (Royauté et al. 2021). According to Royauté et al. (2021), these kinds of sex-specific behavioral syndromes allow the independent evolution of behavioral dimorphism. Though we did not find clear evidence for sex-specific syndromes, the links between functionally different behavioral traits suggest that the sexes differ slightly in the structure of the behavioral syndrome (Figures 4 and 5). In both sexes, individuals with higher activity tended to be more risk tolerant (i.e., have shorter Freezing duration), while the relationship between the first and second trials of the Freezing duration reflected high (short term) intraindividual consistency. More active and bolder females also captured prey faster than the shyer ones, but such a relationship was not found in males (Figures 4 and 5). The same relationship between Activity rate and Capture latency for females, but not for males, was found in *E. militaris* (Royauté et al. 2015). Consistent interindividual differences might coexist with developmental plasticity (Kralj-Fišer and Schneider 2012). Here, both females and males showed consistent interindividual behavioral differences, but we found weaker or undetectable relationships between certain behavioral traits in males compared to the females. This might be explained that sexual maturation can often change the

males' appearance and behavior (Sullivan and Morse 2004; Framenau 2005; Cordellier et al. 2020). Hence, some behavioral traits of *C. xanthogramma* males might be more plastic during development than the behavior of females. In our study, the relationships between the examined traits were usually stronger in females (Table 3 and Figure 4), which contrasted with the general patterns observed in a meta-analytic study (i.e., tend to be stronger in males) focusing on similar behavioral traits in vertebrates (Garamszegi et al. 2012).

The sexes showed similar IIV regarding all of the measured behavioral traits (Table 4). However, using right-censored data (e.g., Freezing duration) might lead to biased estimates of IIV (Stamps et al. 2012), which could eventually result in that sex-specific differences in behavioral predictability remain hidden.

As sexes differ in their life-history optima and reproductive role, unsurprisingly, sexual dimorphism can be observed in certain fitness-related traits and their complex physiological, behavioral, and genetic backgrounds (Hämäläinen et al. 2018; Tarka et al. 2018). The present study implied that even immature females and males might have different life-history strategies with different, sex-specific consequences. Thus, before maturation, females tend to be less active, take less risk, and more sensitive to alarming stimuli than males. In contrast, males could follow a "live fast, die young" life-history strategy. Immature males forage much more intensively to increase their body size faster because selection forces favor the heavier and larger males after maturation.

Acknowledgments

Table 4. Results from linear models, in which the riSD values (a proxy of IIV) of behavioral trait variables of *Carrhotus xanthogramma* immatures ($N = 90$) were the response variables.

Response variable	Predictors	df	Sum of Sq.	Mean of Sq.	F-value	P-value	Effect size (η^2)[*]	CI$_{lower}$	CI$_{upper}$
Activity rate riSD	Site	2	24.95	12.47	0.327	0.722	0.008	NA	0.044
	Sex	1	4.43	4.43	0.116	0.734	0.001	NA	0.039
	Site:Sex	2	33.33	16.66	0.437	0.647	0.010	NA	0.053
	Residuals	84	3,200.52	38.10	NA	NA	NA	NA	NA
Freezing duration, first trial riSD	Site	2	0.49	0.25	0.793	0.456	0.018	NA	0.073
	Sex	1	0.06	0.06	0.195	0.660	0.002	NA	0.045
	Site:Sex	2	0.18	0.09	0.293	0.747	0.007	NA	0.041
	Residuals	84	26.16	0.31	NA	NA	NA	NA	NA
Freezing duration, second trial riSD	Site	2	0.15	0.08	0.369	0.693	0.009	NA	0.048
	Sex	1	0.00	0.00	0.002	0.963	0.000	NA	NA
	Site:Sex	2	0.33	0.17	0.795	0.455	0.018	NA	0.073
	Residuals	84	17.41	0.21	NA	NA	NA	NA	NA
Capture latency riSD	Site	2	41 785.46	20 892.73	1.432	0.245	0.033	NA	0.104
	Sex	1	4,745.51	4,745.51	0.325	0.570	0.004	NA	0.055
	Site:Sex	2	24 643.61	12 321.81	0.844	0.434	0.020	NA	0.078
	Residuals	81	1 182 056.53	14 593.29	NA	NA	NA	NA	NA

[*]Small effect: $0.02 \leq \eta^2 < 0.13$; Medium effect: $0.13 \leq \eta^2 < 0.26$; Large effect: $0.26 \leq \eta^2$.

Funding

Ethics Statement

Our experiments comply with the ASAB/ABS guidelines for the use of animals. We performed experiments with arthropod species that are not protected, and no permission from an ethical committee was needed. We minimized the effect on the population size of the used spiders by reducing sample sizes while maintaining sufficient statistical power.

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