

## RESEARCH PAPER

# The ontogeny of personality traits in the desert funnel-web spider, *Agelenopsis lisa* (Araneae: Agelenidae)

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**Abstract**

Trait consistency over time is one of the cornerstones of animal personality. Behavioral syndromes are the result of correlations between behaviors. While repeatability in behavior is not a requirement for behavioral syndromes, the two concepts studied together provide a more comprehensive understanding of how behavior can change over ontogeny. The roles of ontogenetic processes in the emergence of personality and behavioral syndromes have received much individual attention. However, the characterization of both individual trait consistency and behavioral syndromes across both sexes, as in our study, has been relatively rare. Ontogeny refers to changes that occur from conception to maturation, and juveniles might be expected to undergo different selection pressures than sexually mature individuals and also will experience profound changes in hormones, morphology, and environment during this period. In this study, we test for behavioral trait consistency and behavioral syndromes across six time points during ontogenetic development in the desert funnel-web spider (*Agelenopsis lisa*). Our results indicate behavioral traits generally lack consistency (repeatability) within life stages and across ontogeny. However, penultimate males and mature females do exhibit noticeable mean-level changes, with greater aggressive responses toward prey, shorter latencies to explore their environment and in the exhibition of risk-averse responses to predatory cues. These traits also show high repeatability. Some trait correlations do exist as well. In particular, a strong correlation between aggressiveness toward prey and exploration factors is observed in mature males. However, because correlations among these factors are unstable across ontogeny and vary in strength over time, we conclude that behavioral syndromes do not exist in this species. Nevertheless, our results indicate that increased consistency, increasing average trait values, and varying correlations between traits may coincide with developmentally important changes associated with sexual maturation, albeit at different time points in males and females. This period of the life cycle merits systematic examination across taxa.

**KEYWORDS**

animal personality, behavioral consistency, behavioral syndromes, life history

## 1 | INTRODUCTION

Behavioral biologists have long been interested in the mechanisms by which consistent individual-level differences in behavior may evolve and be maintained over time and/or across contexts. In recent years, this consistency in behavior has been documented in a wide range of taxa and has generally been characterized as representing animal personalities (Dall, Houston, & McNamara, 2004; Réale, Reader, Sol, McDougall, & Dingemanse, 2007). A similar although distinct concept is that of behavioral syndromes, which investigates the manner in which functionally separate behavioral traits are correlated within individuals and populations (Sih, Bell, & Johnson, 2004). Numerous conceptual and empirical advances have been made in this area (Favati, Zidar, Thorpe, Jensen, & Løvlie, 2016; Krause, James, & Croft, 2010; Sweeney et al., 2013; Wilson & Godin, 2009; Wilson, Godin, & Ward, 2010; Wilson & Krause, 2012; Wuerz & Krüger, 2015). However, Stamps and Groothuis (2010a) feel that there remains a need to understand how life-history and developmental processes are integrated with personality. In particular, how both trait variation and correlations change over ontogeny.

Work completed to date on this problem area suggests that behavioral traits and trait correlations showing temporal consistency in adults of a species are not necessarily temporally consistent across ontogeny (Bell & Stamps, 2004; Hedrick & Kortet, 2012; Johnson & Sih, 2007; Niemelä, Vainikka, Hedrick, & Kortet, 2012; Petelle, McCoy, Alejandro, Martin, & Blumstein, 2013; Sinn, Gosling, & Moltschaniwskyj, 2008; Wuerz & Krüger, 2015). Both individual life history and behavior are known to be sensitive to conditions during development. Factors such as temperature, population density, immune challenges, resource availability, and environmental enrichment during development all impact growth rate, maturation time, and body size (Bonenfant, Gaillard, Klein, & Loison, 2002; Metcalfe, Huntingford, Graham, & Thorpe, 1989; Pepin, 1991). For example, both male and female body mass and pregnancy rates of primiparous females increase when population density decreases, with male mass changing to a greater extent than female mass (Bonenfant et al., 2002). Developmental experience can also affect the correlations between different behaviors, as well as the presence/absence of consistent individual differences (Bengston, Pruitt, & Riechert, 2014; Butler, Toomey, McGraw, & Rowe, 2012; DiRienzo & Montiglio, 2016; DiRienzo, Niemelä, Skog, Vainikka, & Kortet, 2015; DiRienzo, Pruitt, & Hedrick, 2012; Günther, Finkemeier, & Trillmich, 2014; Hedrick & Kortet, 2012; McGhee & Travis, 2010; Urszán, Török, Hettyey, Garamszegi, & Herczeg, 2015).

Sexual maturation is another factor associated with behavioral shifts during development (Carere, Drent, Privitera, Koolhaas, & Groothuis, 2005; Dingemanse & Réale, 2005; Small & Schoech, 2015; Videlier, Cornette, Bonneaud, & Herrel, 2015). Transitions between juvenile and adult stages during ontogeny can involve major changes in hormonal profiles, morphology, and environment (Brodin, 2009; Caspi & Roberts, 1990; Relyea & Hoverman, 2003; Riddiford & Truman, 1993; Robertson, 1936; Zera, 2007, 2007). For example, in the Lepidoptera, caterpillars (the juvenile stage) and butterflies (the adult stage) are morphologically dissimilar, while various aquatic

insects develop in the water as larvae but use terrestrial environments as adults (e.g., damselflies; Brodin, 2009). Even in invertebrates such as insects and spiders, in which juveniles and adults have similar morphologies and are more continuous in terms of their development (i.e., they do not undergo metamorphosis), individuals still experience major changes as they mature and we should expect to see resulting differences in behavior.

The dramatic changes associated with sexual maturation suggest that behavioral traits such as boldness might be strongly affected by this event (Stamps & Groothuis, 2010a,b). Interestingly, not all individuals behave similarly and several factors are known to affect an animal's behavior including age and sex (Carere et al., 2005; Dingemanse & Réale, 2005). Differences between sexes may arise as a result of sexual selection (Hedrick & Temeles, 1989) and result in differences in body size (Woolbright, 1983) and other morphological traits (Desjardins & Fernald, 2009). As the energetic cost of gamete production differs between the sexes, this often results in differences in body size and life-history traits (Monroe & Alonzo, 2014). Changes in exploratory trait values and aggressiveness have been shown to occur in the male sex in birds and fish, as well as in male (and less often female) fruit flies (Chen, Lee, Bowens, Huber, & Kravitz, 2002; Sturtevant, 1915). Males may attract females to territories that are defended against intrusion by other males or alternatively wander in search of matings (Brown, Chimenti, & Siebert, 2007; Carere et al., 2005; Dziewczynski & Crovo, 2011). Moreover, hormonal differences between the sexes are likely to impact their exploration and aggression behavior (Baier, Wittek, & Brembs, 2002; Brandner, 2007; Kravitz & Huber, 2003). Future studies should investigate how the aforementioned mechanisms act together across ontogeny, as it is likely that hormones, environmental conditions, and other factors are interacting in concert to produce these behavioral changes.

There are few examples of studies of development of behavioral syndromes in spiders. Boldness and aggression have shown to be uncorrelated in field-caught juvenile grass spiders *Agelenopsis pennsylvanica* (Agelenidae), but a boldness–aggression syndrome manifests at the penultimate stage and the two behavioral traits tested exhibit high repeatability of this syndrome at this stage (Sweeney et al., 2013). A study of the bridge *Larinioides sclopetarius* (Araneidae) failed to detect the presence of a behavioral syndrome at any stage of the life cycle (Kralj-Fišer & Schneider, 2012). While both studies report stability in the measured traits, one species exhibits a behavioral syndrome (Sweeney et al., 2013), while the other does not (Kralj-Fišer & Schneider, 2012). This is interesting because it is shown that repeatability is not a requirement for behavioral syndromes, and there can be trait correlations in a population even with low repeatability. Previous studies have also revealed that a specific experience at a given age affects correlations between traits later in life and that these correlations may change through ontogeny (Carere et al., 2005; Dingemanse et al., 2007; Dingemanse et al. 2009; Bell & Sih 2007; Stamps & Groothuis, 2010a). The critical problem that remains is untangling the effects of genetic, physiological, and environmental cues and how they interact and change across ontogeny to affect trait consistency and behavioral syndromes. In an effort to address this problem, we characterize trait

consistency and behavioral syndromes across ontogeny and sexual maturation in male and female spiders.

In this study, we use a laboratory-reared population of the desert grass spider (*Agelenopsis lisa*) to quantitatively ascertain whether contextual individual-level differences in personality (i.e., activity, boldness, and aggressiveness) are consistent both within a life-history stage (juvenile, penultimate, and adult) and across ontogeny. Specifically, we test the hypotheses that the greatest consistency will be within repeated trials within life stages and that the behavioral traits and trait correlations will change most during the transition to respective mature male and female sexes.

## 2 | METHODS

### 2.1 | Collection and laboratory maintenance

We completed this study on the F1 generation offspring reared in the laboratory from eight families of field collected grass spiders, *Agelenopsis lisa* (Araneae, Agelenidae). Like its close desert relative, *A. aperta*, *A. lisa* occupies arid habitats and builds its sheet web in low vegetation such as in grasses and at the bases of shrubs and cacti. The non-sticky silk sheet is used to sense and locate prey, while the spider sits in the protected environment of its funnel retreat. We collected the parental generation of spiders as late instars along a stretch of tall grass habitat bordering State Hwy 17 at Balmorhea State Park (Balmorhea, TX, 30.944829, -103.785147) during March of 2012. We did not score the behavior of these collected individuals, but merely established each individual in its own container in the laboratory maintained at 22–24°C on a 12:12-hr light: dark cycle. We offered the spiders a diet of *ad libitum* crickets and randomly mated individuals as they matured to produce the F1 generation.

We communally reared the offspring produced by each of the eight matings through the first two instars. We offered these “spiderlings” both termite workers (*Reticulitermes flavipes*) and crickets (*Acheta domesticus*) of appropriate size *ad libitum*. We also weekly misted the communal webs. As individuals molted to the third instar, we assigned them unique identities and moved them from the communal container they had been housed in into individual plastic containers, measuring 11 mm in diameter and 2 mm in height. Our sample turned out to be strongly (3:1) female biased, particularly at the penultimate stage (juveniles:  $n_{\text{female}} = 54$ ,  $n_{\text{male}} = 19$ ; penultimate:  $n_{\text{female}} = 67$ ,  $n_{\text{male}} = 22$ ; and mature:  $n_{\text{female}} = 54$ ,  $n_{\text{male}} = 22$ ).

### 2.2 | Test schedule

We subjected each of 98 of 120 surviving spiders to a battery of 11 behavioral trait tests at three stages in the life cycle: juvenile (third-fifth instar), penultimate (one molt removed from sexual maturity), and sexually mature. Two weeks separated replicate within stage tests. We completed the first trial within a particular life stage seven days following an individual's molt to a new stage and three days after an *ad libitum* feeding.

### 2.3 | Behavioral test trials

We applied the series of behavioral tests developed for examination of ecotypic variation in the behavior of *A. aperta* in this study of *Agelenopsis lisa* (see Riechert and Hedrick (1990, 1993); Riechert and Maupin (1998); Maupin and Riechert (2001); Riechert and Johns (2003) for original descriptions of the tests). The behavioral tests are briefly summarized below in the order in which we completed them.

Seventy-two hours after a routine feeding, we moved the test subject from its home container to a novel container of the same dimensions. We recorded the distance the spider moved before it had ceased movement for five seconds. We then scored the “Latency to start Exploring a Novel Environment” as the time elapsed between cessation of movement and its resumption. After the individual began moving, we measured the amount of time an individual spent active over a 10-min period. Immediately following completion of the activity and boldness assays, we allowed 10 min for habituation before commencing the next test. In the prod track tests, we touched the spider at its posterior or anterior end with the eraser end of a pencil, after Riechert and Johns (2003). We alternated between administering the front prod first or the rear prod first. We recorded (i) the individual's behavior after the prod (run, walk, attack prod, etc.), (ii) the distance travelled around the test arena, and (iii) the time elapsed between the individual's cessation of movement and when the individual began moving again. We allowed the individual five minutes for habituation between the front prod and the rear prod. In each trial, each eraser touched was wiped with a wet paper towel before the next individual's test (to avoid uncontrolled olfactory cues).

Spiders were given twenty-four hours to build a web after completing the boldness trials listed above. After removing the lids from the test arena, spiders were allotted as much time as necessary to appear at their funnel entrance (usually 10–15 min after removing the lid from the container, following Riechert and Hedrick 1990, 1993). We held a camera-cleaning bulb at a 45° angle to the web, at a height of eight cm and directed a single puff of air at a spot six cm in front of the funnel entrance. We recorded (i) the spider's response to the puff (whether it displayed an aggressive response such as running out toward the cue or a fearful/non-aggressive response such as retreating into the funnel) and (ii) the length of time that elapsed between retreat and the reappearance of the spider at the funnel entrance. No retreat or aggressive responses were scored as 0 s.

After the puff test, spiders were given 10 min to habituate before completing the tests of aggression toward prey. We offered the individual a single two-week-old cricket. The cricket was placed on the web approximately 2.0 cm from the test individual, and the latency to attack (make contact with the prey) was recorded. The superfluous killing trials followed the protocols developed previously Riechert and Maupin (1998) and Maupin and Riechert (2001) to test for general foraging aggressiveness. Crickets were introduced, one at a time, at three-minute intervals to the individual's web. Additional time was provided if an individual needed more time to subdue its prey. Trials were terminated when an individual failed to attack two consecutive prey items. At the end of the observation period, all rejected prey

items were removed from the web, and the individual was given 24 hr to feed on the prey. After this 24-hr period, the captured prey items were assigned to one of the following categories based on the remaining percentage of mass relative to their original body mass: fully consumed (<10%), partially consumed (10%–25%), or uneaten (>25%). If an individual was feeding on prey after 24 hr, it was given an additional 24 hr to feed and the prey identified as to feeding classification after that time. The capture estimate is a measure of how many prey items an individual captured while the wasteful killing estimate is a measure of the overall amount of prey actually consumed by the individual spider. Descriptions of these calculations are available in Riechert and Maupin (1998) and Maupin and Riechert (2001).

## 2.4 | Statistical analyses

### 2.4.1 | Factor analysis

All 11 measures from the behavioral assays were scaled and centered to zero and entered into an exploratory factor analysis. We used exploratory factor analysis rather than PCA because our main aim was to determine and assess unobservable behavioral constructs rather than to simply reduce the number of dimensions (Budaev, 2010). In short, we sought to identify the dimensions of animal personality in this species. Although the full data set included variable numbers of repeat measures per individual (individuals were measured 1–6 times), restricting the factor analysis to the first measurement of each individual did not alter the number of factors extracted or the factor loadings on them. Only extracted factors with eigenvalues larger than one were retained for further analyses.

### 2.4.2 | Linear mixed effects models

We assessed the role of sex and life stage during ontogeny on life-history variables using linear mixed models. The four factors extracted from the exploratory factor analysis were response variables. Individual and mother ID were tested as the only random effects in addition to the fixed effects of trial number, sex, developmental life stage, and the sex\*developmental life-stage interaction. There were two categories in the sex fixed effect (male and female) and three categories in the developmental life-stage fixed effect (juvenile, penultimate, and mature). These mixed models were fit with the “LME4” package (Bates, Maechler, Bolker, & Walker, 2014). Residuals of the models were visually inspected for homogeneity of variances and normal distribution by using Q–Q plots and histograms.

We calculated the adjusted repeatability of the four factors following the methods of Nakagawa and Schielzeth (2010) using the *rptR* package (Schielzeth & Nakagawa, 2013). Across life-stage repeatabilities were calculated using the variance components of the fully parameterized models described in the previous paragraph. Within life-stage repeatabilities were calculated using the variance components from models with the same structure as the across life-stage models, with the random effects of individual and mother ID, minus the main effect of developmental life stage and fitted to only the appropriate subset

of data (e.g., juvenile male, juvenile female, penultimate male, penultimate female, mature male, or mature female only). We also performed additional repeatability calculations across two life stages for both males and females (juvenile to penultimate and penultimate to mature). Through parametric bootstrapping procedures, 95% confidence intervals were obtained (number of simulations = 1000) (Bates et al., 2014).

To account for multiple testing (we assessed 28 “lmer” models in total and 44 “rptR” models), we applied false discovery rate (FDR) adjustment (Benjamini & Hochberg, 1995). We did not use a Bonferroni correction to adjust the *p*-values for multiple comparisons as it tends to be overly conservative and can lead to an increase in type II error. Instead, we employed the false recovery estimate of Benjamini and Hochberg (1995). This method controls the expected proportion of false discoveries (rejected hypotheses). The discovery rate is a less-stringent condition than the family-wise error rate employed by methods such as the Bonferroni correction. Thus, it is more powerful in minimizing type I and II errors when many pairwise comparisons are conducted. For all six developmental stages, to estimate correlations between the different factors, we took the average of the two scores present for each life stage (or used the first trial if only one score was present) and applied Spearman correlations. For each of the six stages, we calculated six correlations and again corrected for multiple testing by applying FDR. We also computed a Spearman rank correlation matrix for each age to test for structural consistency (i.e., whether correlation structures of behavioral responses change over time and developmental stages). We also applied Mantel randomization tests with 10,000 permutations to determine whether correlation structures were similar for males and females at each time point. *R* version (3.2.4) was used for all statistical analyses (Team 2014), and the package “ADE4” v1.7-4 was used for the Mantel randomization test (Dray & Dufour, 2007).

## 3 | RESULTS

### 3.1 | Factor analysis

The factor analysis on the behavioral data produced four factors with eigenvalues >1 (Table 1). Higher scores on the first factor (FA1, 18% of the total variation) implied higher capture estimates and higher wasteful killing estimates, which reflect foraging behaviors. Higher scores on the second factor (FA2, 16% of the total variation) implied longer distances traveled upon introduction to a novel environment, longer distances traveled upon being prodded from the front, and longer distances traveled upon being prodded from the rear. Factor 2 reflects the distances traveled in the prod (predatory cue) and exploration trials. Higher scores on the third factor (FA3, 12% of the total variation) implied longer latencies to start exploring a novel environment, longer latencies to return to exploring after a front prod, and longer latencies to start exploring after a rear prod. Factor 3 reflects the latencies to act in the prod and exploration trials. Higher scores on the fourth factor (FA4, 9% of the total variation) implied longer latencies to return to a foraging position after a predatory puff cue, which is a cue that

	FA1	FA2	FA3	FA4
Eigenvalue	1.991	1.758	1.288	1.041
Proportion of variance explained	18.10%	15.983%	11.708%	9.459%
Distance traveled upon introduction to novel environment	0.191	<b>0.385</b>	-0.042	0.184
Latency to start exploring novel environment	-0.025	0.048	<b>0.411</b>	0.153
Activity over 10 min	0.148	-0.143	-0.246	-0.086
Distance traveled after front prod	0.028	<b>0.744</b>	0.028	-0.092
Latency to start exploring after front prod	0.037	0.010	<b>0.482</b>	0.137
Distance traveled after rear prod	0.054	<b>0.507</b>	0.122	0.024
Latency to start exploring after rear prod	-0.026	0.000	<b>0.605</b>	-0.149
Latency to return after puff	-0.019	0.026	0.139	<b>0.410</b>
Latency to capture prey	-0.202	-0.033	-0.043	0.082
Prey capture estimate	<b>0.980</b>	0.035	-0.119	0.002
Wasteful killing estimate	<b>0.638</b>	0.159	-0.114	0.174

Factor loadings with an absolute correlation of  $>0.3$  are shown in bold. Seven further extracted axes (not shown) each explained  $<10\%$  of the total variation in behavioral measures.

simulates the approach of a predator. Latency to capture the first prey item did not load on any of the four factors and was excluded from any further analyses.

### 3.2 | Influence of life stage on personality type

Table 2 shows the full mixed effects models for each of the four extracted factors. Factor 4 scores for mature males were significantly higher than juvenile females ( $\beta = 0.54 \pm 0.15$ ; see Table 2). Factor 4 scores for the other life stages were not significantly different from juvenile females (used as the reference groups for the interaction term). Trial number, sex, developmental stage, and sex\*developmental stage had no effect on Factor 1, 2, or 3 scores.

### 3.3 | Development of personality structure

After correcting for multiple comparisons, only the prod test scores (Factor 2) were significantly repeatable across the entire life cycle ( $R = 0.13$ , 95% CI: 0.05–0.24,  $p = .0017$ ). Scores for Factor 1, Factor 3, and Factor 4 were not significantly repeatable across the life cycle. None of the factors were significantly repeatable within an individual developmental stage. However, the aggressiveness toward prey scores (Factor 1) were significantly repeatable in penultimate + mature males ( $R = 0.62$ , 95% CI: 0.26–0.80,  $p = .0006$ ) but were not significantly repeatable within the individual penultimate or mature male stages. The boldness toward puff scores (Factor 4) was significantly repeatable in juvenile + penultimate

**TABLE 2** Linear models predicting the effect of sex, instar, sex\*instar, and trial on 98 individuals (number of observations = 396) for all fixed effects included in four linear mixed models for the FA axes (FA1, FA2, FA3, and FA4) with eigenvalues  $>1$

Effect	FA1		FA2		FA3		FA4	
	$\beta \pm SE$	$p$	$\beta \pm SE$	$p$	$\beta \pm SE$	$p$	$\beta \pm SE$	$p$
Intercept	$0.20 \pm 0.12$	.08	$0.24 \pm 0.14$	.12	$0.03 \pm 0.11$	.78	$0.23 \pm 0.06$	$<.001$
Trial number	$-0.02 \pm 0.04$	.69	$-0.07 \pm 0.04$	.12	$0.01 \pm 0.04$	.70	$-0.05 \pm 0.03$	.05
Sex <sup>a</sup>								
Male	$-0.14 \pm 0.20$	.50	$-0.30 \pm 0.20$	.13	$-0.20 \pm 0.18$	.26	$-0.16 \pm 0.12$	.17
Instar <sup>b</sup>								
Penultimate	$-0.08 \pm 0.15$	.59	$0.15 \pm 0.12$	.24	$0.08 \pm 0.12$	.51	$-0.16 \pm 0.08$	.05
Mature	$-0.23 \pm 0.18$	.21	$-0.09 \pm 0.17$	.58	$-0.03 \pm 0.16$	.84	$-0.20 \pm 0.10$	.05
Sex*Instar <sup>c</sup>								
Penultimate male	$0.58 \pm 0.28$	.02	$-0.14 \pm 0.22$	.53	$0.02 \pm 0.21$	.93	$0.21 \pm 0.16$	.19
Mature male	$-0.63 \pm 0.27$	.04	$0.47 \pm 0.22$	.03	$0.55 \pm 0.21$	.01	$0.54 \pm 0.15$	$<.001$

<sup>a</sup>Reference category is "female."

<sup>b</sup>Reference category is "juvenile."

<sup>c</sup>Reference categories are "female" and "juvenile."

**TABLE 3** Repeatability estimates, *p*-values (produced by likelihood ratio tests), and 95% confidence limits within and across life stages for the four extracted factors

Trait	Life stage	$R_{adj}$	CI (95%)	<i>p</i>
FA1	All	0.02	0, 0.11	.33
	Juvenile male	0	0, 0.71	.50
	Juvenile female	0	0, 0.30	.5
	Penultimate male	0.63	0, 0.94	.01
	Penultimate female	0.02	0, 0.29	.50
	Mature male	0	0, 0.48	.50
	Mature female	0.27	0.02, 0.54	.02
	Juvenile + Penultimate male	0	0, 0.30	.5
	Juvenile + Penultimate female	0	0, 0.12	.5
	Penultimate + Mature male	0.62	0.26, 0.80	.0006
	Penultimate + Mature female	0.17	0.03, 0.32	.01
FA2	All	<b>0.13</b>	<b>0.05, 0.24</b>	<b>.0017</b>
	Juvenile male	0	0, 0.68	.50
	Juvenile female	0.21	0, 0.50	.05
	Penultimate male	0.83	0.31, 0.97	.01
	Penultimate female	0	0, 0.23	.50
	Mature male	0.25	0, 0.70	.17
	Mature female	0	0, 0.28	.50
	Juvenile + Penultimate male	0.44	0.07, 0.68	.0057
	Juvenile + Penultimate female	0.11	0, 0.26	.03
	Penultimate + Mature male	0.16	0, 0.43	.13
FA3	All	0.10	0.01, 0.20	.01
	Juvenile male	0	0, 0.66	.50
	Juvenile female	0	0, 0.25	.50
	Penultimate male	0	0, 0.79	.50
	Penultimate female	0.03	0, 0.31	.43
	Mature male	0	0, 0.46	.50
	Mature female	0.09	0, 0.36	.20
	Juvenile + Penultimate male	0.18	0, 0.50	.15
	Juvenile + Penultimate female	0.10	0, 0.24	.07
	Penultimate + Mature male	0	0, 0.26	.50
	Penultimate + Mature female	0.14	0, 0.28	.04

(Continues)

males ( $R = 0.35$ , 95% CI: 0.03–0.65,  $p = .0019$ ) but was not significantly repeatable within the individual juvenile or penultimate male stages (Table 3).

The only significant correlation is a positive correlation between Factor 1 and Factor 3 in mature males ( $\rho = 0.58$ ,  $p < .001$ , 95% CI: 0.21–0.80). All pairwise Spearman correlations are found in Figure 1.

**TABLE 3** (Continued)

Trait	Life stage	$R_{adj}$	CI (95%)	<i>p</i>
FA4	All	0.05	0, 0.14	.09
	Juvenile male	0.22	0, 0.75	.50
	Juvenile female	0.12	0, 0.40	.21
	Penultimate male	0.51	0, 0.88	.04
	Penultimate female	0.23	0, 0.49	.13
	Mature male	0	0, 0.54	.50
	Mature female	0.24	0, 0.52	.06
	Juvenile + Penultimate male	0.35	0.03, 0.65	.0019
	Juvenile + Penultimate female	0.05	0, 0.18	.22
	Penultimate + Mature male	0.03	0, 0.31	.40
	Penultimate + Mature female	0.02	0, 0.16	.39

*p*-values presented are corrected for multiple comparisons. Repeatabilities that had a *p*-value  $< .05$  after adjustment of *p*-values are bolded.

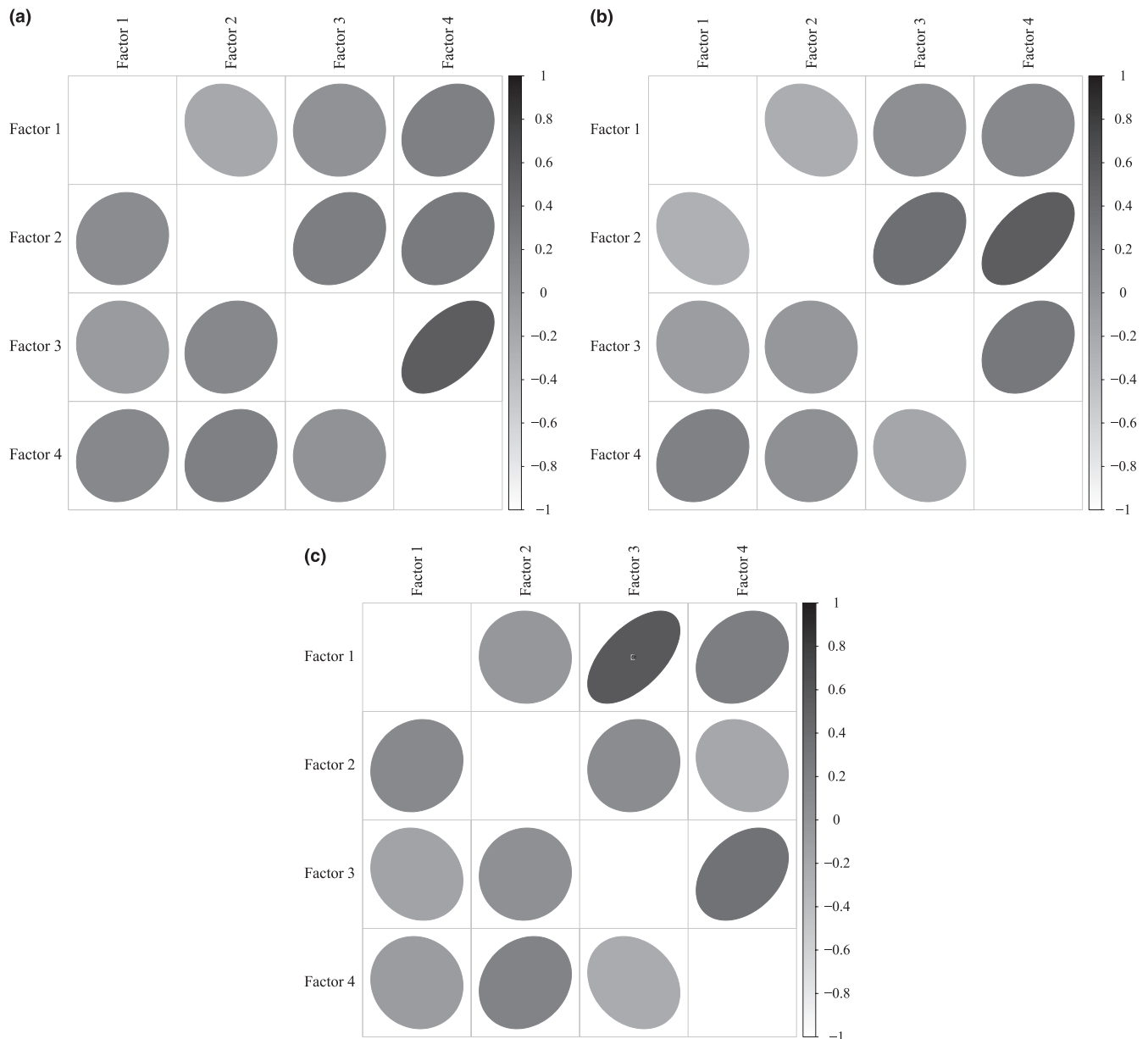
All of the pairwise Mantel tests between the correlation matrices (Table 4) are not significant. This result indicates that the correlational structure of the measured variables is dissimilar across life stages. A comparison of correlation matrices between subsequent time points reveals that the relationship between the extracted factors changes during ontogeny from juvenile to adult in both sexes (Table 4).

## 4 | DISCUSSION

This study is the first both to characterize a large number of behavioral traits and to provide measures of consistency of behavioral traits across such a large portion (~75%) of the life cycle in both sexes in any invertebrate species (but see Kralj-Fišer and Schneider 2012 and Sweeney et al. 2013 for other ontogenetic studies of behavioral consistency in spiders).

We identified the clustering of the ten traits we measured in *A. lisa* into four behavioral factors, the first (Factor 1) reflecting foraging behaviors, the second (Factor 2) distances traveled in prod (predatory cue) and exploration trials, the third (Factor 3) latencies to act in these trials and the fourth (Factor 4), response to a puff cue that simulates the approach of a predator. The mean expression and repeatability of each of these factors, as well as the structure of behavioral syndromes, tend to vary across different developmental stages. Thus, we conclude that behavioral syndromes are not consistent in structure across life stages. This could be an artifact of having small sample sizes for males because our sample turned out to be strongly (3:1) female biased, while testing within unknown positions in the molt cycle may also have produced noise in these analyses. However, this inconsistency may suggest that different life stages have shifting ideal behavioral structures instead of one behavioral repertoire being sufficient across ontogeny.





**FIGURE 1** Spearman rank correlations for four extracted factors across life stages. Spearman rank correlation coefficients are given for females (below diagonal) and males (above diagonal), (a) juveniles:  $n_{\text{female}} = 54$ ,  $n_{\text{male}} = 19$ , (b) penultimate:  $n_{\text{female}} = 67$ ,  $n_{\text{male}} = 22$ , and (c) mature:  $n_{\text{female}} = 54$ ,  $n_{\text{male}} = 22$ . Correlations that had a  $p$ -value  $< .05$  after adjustment of  $p$ -values are marked with (\*). Significance at the  $*p < .05$  after adjusting  $p$ -values for multiple comparisons

#### 4.1 | Major shifts associated with risk-averse vs. risk-prone strategies

Our results suggest that a major shift in behavior from risk-averse to risk-prone trait values occurs in males as they reach the penultimate stage one molt removed from sexual maturity and in females following maturation. Penultimate males show higher aggressiveness toward prey (Factor 1) and speedier returns to activity such as foraging and exploration following their initial response to a predatory cue (Factors 3 and 4). The mass a penultimate male achieves is ultimately associated with its mating success as demonstrated for desert *A. aperta*, a close relative of *A. lisa* (Singer & Riechert, 1995). Male *A. aperta* abandon

feeding shortly after maturity. Larger body mass is a significant determinant of (i) the length of time a male can travel in search of matings, (ii) success in male/male contests over access to females, and (iii) being accepted by a female. Female *A. lisa* exhibit similar shifts in behavior to males, but they occur following sexual maturation and are associated with accumulating the resources needed for egg production. Female fecundity is strongly correlated with body mass in *A. aperta* (Riechert & Johns, 2003). Therefore, we conclude that the shift from a risk-averse to a risk-prone behavioral strategy coincides with the different transitions that occur during sexual maturation in males and females.

The above shifts from risk-averse strategies in juveniles to risk-prone strategies associated with the need to gain mass in preparation

**TABLE 4** Structural consistency of the relations among the four factors in *Agelenopsis lisa*

Distance matrices	$r_s$	$p$
Juvenile male vs. juvenile female	0.13	.13
Penultimate male vs. penultimate female	0.49	.12
Mature male vs. mature female	−0.91	.96
Juvenile male vs. penultimate male	0.76	.09
Juvenile male vs. mature male	0.10	.46
Penultimate male vs. mature male	−0.24	.63
Juvenile female vs. penultimate female	0.47	.16
Juvenile female vs. mature female	0.76	.05
Penultimate female vs. mature female	0.03	.41

Pairwise Mantel tests between rank correlation matrices ( $r_s$ ) of factor scores and their significance ( $p$ -value) at different life stages.

for reproduction have been observed in other species as well (Dangles, Pierre, Christides, & Casas, 2007; Favati et al., 2015; Hedrick & Kortet, 2012). However, see Gyuris, Feró, and Barta (2012) for an example of risk-prone feeding behavior observed in juvenile firebugs. Shifts between the two strategies in behavior reflect different selection pressures that are encountered during the life cycle of particular species and likely reflect a compromise between the need for increasing mass vs. avoiding predation (Hoverman & Relyea, 2016; Macleod, Barnett, Clark, & Cresswell, 2005).

## 4.2 | Behavioral trait consistency

We found that behavioral trait consistencies are generally quite low across the ontogenetic development of *A. lisa*. The exceptions are our second factor (Factor 2) distances traveled in prod (predatory cue) and exploration trials. These are the only traits that show significant repeatability across the life cycle. These traits show particularly high repeatability in penultimate males and mature females. While not meeting significance levels in any individual group, aggressiveness toward prey traits (Factor 1) and the predator response to a puff cue factor (Factor 4) exhibit the same repeatability pattern. However, the penultimate + mature males show significant for Factor 1, and juvenile + penultimate males show significant repeatability for Factor 4. These high repeatability estimates are due to high across-individual variation and low within-individual variation. In contrast, the low repeatability estimates across most of the life cycle result from low across-individual variation, meaning that all individuals are generally doing the same thing. These results reflect the fact that individual variation in these factors is reduced across metamorphosis in males, while maintained in penultimate males and females, for reasons described in the previous section: Males wandering in search of matings are exposed to higher risks of predation than females that occupy the protected environment of the funnel web. These same results reflect the fact that individual variation in these factors was reduced across metamorphosis in males (all males converged on lower aggressiveness toward prey and more fearful responses toward predator cues) but was preserved in females. Higher risks of predation or competition

with other males compared to females because of their abandonment of the web may be responsible for this pattern. Additionally, as female fecundity is strongly correlated with body mass, females may be selected to continue acquiring resources at a high rate after becoming reproductive. Schuett and Dall (2009) predicted that females should be more consistent in their foraging intensity than males because reproduction is more energetically costly for females. A similar trend was found in crickets where boldness was found to be significantly repeatable across metamorphosis in females, but not males (Hedrick & Kortet, 2012). However, the same argument could be made in this case for penultimate males because male reproductive success is also strongly correlated with body mass. As mature males decrease their foraging intensity to search for females, penultimate males should be more consistent in their foraging intensity to gain more mass in preparation for maturation. Inconsistency in behavior across sexual maturation has also been demonstrated for boldness in dumpling squid (Sinn et al., 2008), zebra finches (Wuerz & Krüger, 2015), and crickets (Hedrick & Kortet, 2012; Niemelä et al., 2012), and superfluous killing and courtship in bridge spiders (Kralj-Fišer & Schneider, 2012).

Reports to date on personality shifts across ontogeny and over longer periods of the life history of a species indicate that some aspects of personality are set early in life (Gyuris et al., 2012; Mazué, Dechaume-Moncharmont, & Godin, 2015; Wilson & Krause, 2012), whereas other aspects of personality are unstable across ontogeny (Bell & Stamps, 2004; Hedrick & Kortet, 2012; Johnson & Sih, 2007; Niemelä et al., 2012; Petelle et al., 2013; Sinn et al., 2008; Wuerz & Krüger, 2015). Consistent with our study, Wuerz and Krüger (2015) noted that traits can be repeatable across the life cycle (i.e., fearlessness/boldness) or only consistent within certain life stages between sexes (aggression, exploration, and activity), which is within the range of repeatabilities described in general (Bell, Hankison, & Laskowski, 2009; Wolak, Fairbairn, & Paulsen, 2012).

Unlike our study, however, there are studies that suggest individual behavior becomes more consistent following maturity (Favati et al., 2015; Gyuris et al., 2012; Roberts, Caspi, & Moffitt, 2001; Sinn et al., 2008). One potential explanation for observed consistency in behavioral traits across ontogeny (even if seemingly maladaptive) is that some traits may have a genetic (i.e., pleiotropic) or physiological (i.e., hormonal and metabolic) basis that is difficult to uncouple over ontogeny (Sih et al., 2004). Two examples of behavioral consistency across metamorphosis are lake frogs (Wilson & Krause, 2012) and damselflies (Brodin, 2009). Such factors may independently be responsible for observed behavioral consistencies or form behavioral syndromes that persist across metamorphosis, in spite of the dramatic morphological and physiological changes occurring (Wilson & Krause, 2012). Studies are needed that investigate the contributions of hormonal reorganization during sexual maturation vs. the role of diverging natural and sexual selection pressures between sexes in generating observed levels of behavioral consistency.

## 4.3 | Trait correlations

A key element of behavioral syndromes is the potential correlation among behavioral traits. The results of our study completed on *A. lisa*



support the idea that behavioral syndromes may be plastic and not mainly due to genetic constraints (Dingemanse et al., 2007; Johnson & Sih, 2007). For example, we did not find that individuals who are more aggressive toward prey are also quicker to resume exploration after predatory stimuli. In fact, we found the opposite is the case for mature male *A. lisa*, but this result may reflect the fact that we caught them in the transition between states of which production of a molt is only indicative. A similar observation has been made in domestic red jungle fowl and yellow-bellied marmots in that behavioral syndromes did not appear across major life transitions (Favati et al., 2015; Petelle et al., 2013), even though previous studies noted that correlations among traits changed over ontogeny in red jungle fowl (Favati, Leimar, & Løvlie, 2014; Favati, Leimar, Radesäter, & Løvlie, 2014). If selective pressures change drastically throughout ontogeny, one would expect that correlations between behaviors change in response. For example, in penultimate males, individuals that exhibit increased aggressiveness toward prey tend to be quicker to resume exploration after predatory stimuli. This coincides with the more risk-prone strategy discussed above. However, the opposite is true in mature males. Without the protection and sensory capabilities of the prey capture web, males should be more cautious in response to potential predatory cues, but more aggressive toward prey that they encounter less frequently. This conclusion raises the possibility that decreased boldness and increased aggressiveness toward prey may be adaptive in some situations, a possibility rarely brought up in studies of behavioral syndromes. Studies with other test systems have identified experience as playing a key role in generating individual consistency of behavioral traits and behavioral syndromes. For example, behavioral syndromes failed to appear without exposure to cues from predators in *Rana dalmantina* (Urszán et al., 2015) and *Gasterosteus aculeatus* (Bell & Sih 2007).

In conclusion, we found that in contrast to the idea of behavioral syndromes, there was little consistency in behavior across life stages in the desert grass spider *Agelenopsis lisa*. These correlations are not manifest through development. The process of sexual maturation appears as an event decreasing repeatability in personality during ontogeny. During this period, all individuals behaving in the same way are driving increased consistency, but low across-individual variation is driving low repeatability. In addition to that, the influence of these events differed among the behavioral traits studied here. In contradiction to the lack of a correlation structure presented here, previous studies on laboratory-reared *Agelenopsis aperta* have found consistent individual differences and behavioral syndromes to exist in that species when scored at penultimate and adult stages (e.g., Riechert, Singer, & Jones, 2001). The underlying mechanisms of the physiologically, environmentally, and socially generated consistency and change remain unclear. Our results and those of other systems completed to date emphasize the need for future studies that are designed to disentangle internal (e.g., physiology/hormones, molt cycle variation) and external (e.g., social reorganization, environmental) factors that operate during ontogenetic development to better understand the underlying processes responsible for the observed organization and stability of personality traits in individuals collected from the field.

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