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Individual behavioural consistency and plasticity in an urban spider

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Behaviour is generally plastic to some degree and allows an animal to react appropriately to changing and novel conditions. Consequently, a degree of plasticity is predicted to be a key determinant of an organism's ability to cope with novel (e.g. urban) environments. Yet behavioural plasticity is often genetically determined and many animals exhibit personalities (i.e. consistent between-individual differences in behaviours). We explored the degree of behavioural plasticity versus personality in the bridge spider, *Larinioides sclopetarius*, which occurs in extremely high densities in urban areas over the Holarctic. The spiders show extraordinary plasticity in life history. We investigated between- and within-individual variability, correlations and heritability for aggressiveness, boldness, behaviours in novel environment, and voracity towards prey. We predicted that these spiders would show high individual behavioural plasticity or that there would be a mix of individuals with different personalities. We found temporal consistency and moderate heritability in intra-sex aggressiveness and boldness, whereas behaviours in novel environment were repeatable but not heritable. Most behavioural traits showed high between-individual variability. We discuss the idea that low heritability of behaviours related to foraging success and a lack of behavioural correlations may be a result of developmental plasticity as a mechanism that promotes success in cities. In the next step, we experimentally tested whether composition of aggressiveness types affects spiders' mass gain and survival in a high-density group. Groups of only aggressive types had highest mass but also showed highest mortality, although not significantly. Our results lend support to the hypothesis that living in high densities does not necessarily require a reduction of mean aggressiveness levels but that a polymorphism in aggressive personalities maintained by negative frequency-dependent selection would be a possible scenario.

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Urbanized environments are a progressively prominent feature of the earth's ecosystems. Urbanization has caused habitat alterations, pollution and changes in sensory stimuli, which lead to changes in biodiversity and community structure (Bonier et al. 2007; Godefroid & Koedam 2007). Most species have failed to tolerate environments that are altered and disturbed by humans; yet some species do persist and even thrive in cities (Møller 2010; Sih et al. 2011). Similarly to invasive species, many urban species can proliferate rapidly, increase in abundance in a short time, outcompete other less tolerant species and become locally dominant (Kolar & Lodge 2001; Colautti & Maclsaac 2004). Despite the countless ecological problems and large economic costs related to urban species, the characteristics distinguishing the species that flourish in the cities are poorly understood.

The bridge spider, *Larinioides sclopetarius* Clerck (Araneidae), is an extremely successful colonizer of urban areas over the Holarctic

(Heiling 1999; Schmitt 2004; Schmitt & Nioduschewski 2007). In this study we sought to explain its success in cities from a behavioural plasticity point of view, and tested predictions of two non-mutually exclusive hypotheses: (1) *L. sclopetarius* is a successful dweller of urban environments because of a high degree of behavioural plasticity; and/or (2) *L. sclopetarius* is a successful urban dweller because the population exhibits polymorphism in personalities, in particular in aggressiveness types.

Previous studies have identified traits related to species' abilities to cope well in anthropogenic environments, such as fast growth and a short reproductive cycle, high mobility, high aggressiveness and activity, low neophobia (boldness), high phenotypic plasticity and tolerance to a wide range of environmental conditions (Lodge 1993; Sol et al. 2002; Rehage & Sih 2004; Snyder & Evans 2006; Pintor & Sih 2009; Cote et al. 2010, 2011; Møller 2010; Evans et al. 2011). A behavioural response to a change depends on the behavioural reaction norm (i.e. the set of behavioural phenotypes that a single individual produces in a given set of environments; Stamps & Groothuis 2010). The reaction norm and its plasticity is genetically determined and thus a result of past evolutionary processes (Pigliucci 1998). Hence, animals from urban environments are

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likely to encompass high plasticity in behavioural reaction norms, which would allow them to cope with new and variable city environments (Shochat et al. 2006; Kleinteich & Schneider 2010; Tuomainen & Candolin 2011). However, high behavioural plasticity may not always be possible, as evidence is accumulating that many animals exhibit personalities (i.e. consistent interindividual differences in behaviours over time and across contexts; Groothuis & Carere 2005; Bell et al. 2009). In this context, individuals within populations commonly show high between-individual, but low within-individual, variability in behaviours such as aggression, activity, exploration and boldness (Gosling 2001; Sih et al. 2004). These personality traits are commonly intercorrelated and form behavioural syndromes, are (moderately) heritable and are linked to fitness traits (Sih et al. 2004; van Oers et al. 2005; Reale et al. 2007).

Recent theoretical work has shown that polymorphism in behavioural traits can be maintained by negative frequency-dependent selection (Eliassen et al. 2006; Wolf et al. 2007, Wolf & Weissing 2010). Under negative frequency selection, a population should evolve to an equilibrium state in which the different behavioural types have the same fitness expectations (Maynard Smith 1982). A stable coexistence of different behavioural types may be facilitated when each behavioural type has a fitness advantage when rare; when individuals facing an unpredictable environment play a bet-hedging strategy, or when different behavioural types complement each other in a synergistic way (Wolf et al. 2007, Wolf and Weissing, 2010). Along similar lines, a model proposed by Fogarty et al. (2011) suggests that different behavioural types, e.g. shy and bold, might be favoured in different stages of an invasion process. According to this model (Fogarty et al. 2011), good dispersers tend to be bolder, more aggressive and less sociable (Fraser et al. 2001; Cote & Clobert 2007; Cote et al. 2010, 2011), whereas social or nonaggressive individuals may cause a population to grow rapidly to high density and impact on the native community (Cote et al. 2011). Hence, coexistence of social (nonaggressive) and asocial (aggressive) individuals is expected to promote the spread of an invasive species (Fogarty et al. 2011). The spread of urban dwellers may to some extent parallel invasion scenarios, and the same logic may apply.

By contrast, it is possible that selection has favoured individuals with personalities suitable for life in urban areas. For example, aggressive individuals commonly do not adapt their behaviour to the social context (i.e. they have a relatively narrow behavioural reaction norm), for example high density, whereas less aggressive individuals do (i.e. they have a relatively wide behavioural reaction norm). Within this framework, more aggressive individuals are predicted to be favoured in stable conditions, whereas less aggressive individuals are expected to be favoured in fluctuating environments (Koolhaas et al. 2001). From this perspective, urban populations should exhibit low between-individual variability and relatively high individual behavioural plasticity.

To unravel the interplay between behavioural plasticity and flexibility in the bridge spider, we tested wild-caught and laboratory-bred individuals for between- and within-individual behavioural variability, behavioural correlations (behavioural syndromes) and behavioural heritability. In particular, we were interested in the relevance of a mixture of behavioural types to their fitness in high-density conditions. This is because *L. sclopetarius* aggregate in large numbers: up to 100 individuals per m² (Nioduschewski & Kraayvanger 2005). Hence, high intraspecific aggressiveness is expected to be selected against because it probably leads to high mortality.

Intra-individual behavioural plasticity, or rather the lack of it, and (moderate) heritability that characterize personalities are commonly statistically determined by repeatability and mid-parent

regression, respectively (Falconer 1996; Roff 2002). However, we are not aware of any study that tried to evaluate another characteristic of personalities (i.e. between-individual variability by statistical means). Here, we assumed that between-individual variation in behaviour is significant when the quartile coefficient of dispersion is higher than 0.5 (see Methods).

METHODS

Study Animals

Larinioides sclopetarius is a nocturnal orb-weaver that lives near water bodies. The species has successfully colonized human constructions close to water in all places in the Holarctic (Heiling & Herberstein 1998). Populations appear in very high densities, consisting of individuals of different sexes and ages (Heiling & Herberstein 1998). Despite the high density of individuals, these spiders are still territorial and do not build communal webs (Heiling & Herberstein 1998). Although webs can be very close to one another, individuals are regularly observed to compete for profitable web sites and aggressive intrusions of webs, as well as cannibalism, are common (personal observations). During the day *L. sclopetarius* hides in crevices.

In September 2010 we collected subadult spiders in the areas along riverbanks in Hamburg, Germany. The subadult spiders were kept in 200 ml plastic cups and fed with *Drosophila* spp. until adulthood. Upon maturation, males ($N = 31$) remained in the 200 ml cups under the same feeding treatment, whereas adult females ($N = 30$) were transferred into plastic frames (36 × 36 cm and 6 cm high) and fed with *Calliphora* spp. Throughout the study we fed the spiders twice a week, watered using a spray bottle 5 days a week and kept them at room temperature under 10:14 h light:dark conditions.

Experimental Design

All spiders were weighed to an accuracy of 0.01 mg when matured and then subjected to the below experiments.

Personality characterization

We observed the behaviour of spiders in a series of standardized tests for personality characterization (i.e. novel environment test: behaviours related to activity in novel environment; predatory test: boldness; contest: aggressiveness to a same-sex conspecific; feeding: aggressiveness towards prey, superfluous killing (only females); and mating: aggressiveness towards a mate and sexual cannibalism (females), and courtship, boldness towards female (males)). All individuals were tested twice, within 7 days, in each of the test situations. The order of the tests was randomized.

Behaviours related to activity in the novel environment

A spider was carefully placed in an unfamiliar plastic container (11 × 11 cm and 6 cm high) using a paintbrush. Generally, the spider immediately started to move around the container. In the next 5 min we recorded the latency to the first halt and the latency to move again after the first halt.

Predatory test

A spider was gently placed in the plastic container (11 × 11 cm and 6 cm high). Subsequently, we simulated a predator attack by shaking the container until the spider feigned death. This behaviour is characterized by curling legs and freezing, resulting in a body posture very similar to that of a dead spider. We defined the time that elapsed between the start of death feigning to the first move afterwards as boldness. A spider was considered to be feigning

death only if the condition lasted longer than 3 s. Trembling legs was not considered to represent a 'move'.

Aggressiveness towards same-sex conspecific

We tested both male and female aggressiveness by placing two individuals of the same sex close to each other, and we recorded their behaviour for 20 min. Contestants were weight-matched to the average difference of 15.11% and 7.93% in females and males, respectively. Generally the female resident was found in a retreat, in a corner of the frame. The intruder was then carefully placed with the aid of a paintbrush approximately 5 cm away from the resident in the web. Females were tested twice, once as residents in their own web and once as intruders on an unfamiliar web. We randomly selected females to be tested in the role of the intruder or as the resident first.

Males give up web building when adult. To observe males in a competitive situation, two males were placed on a female web. Males were placed in the centre of the female web, approximately 5 cm from each other, while the female was sitting in her retreat. Aggressiveness was measured as a score based on the frequency of aggressive behaviour such as approaching (score = 1), web shaking (score = 1), attacking (score = 2), chasing (score = 3) and biting (score = 3) (Kralj-Fišer et al. 2012). 'Approach' was defined as a movement by one spider towards the other individual, and 'chasing' as a quick move in the direction of the other individual, resulting in a successful attack or escape.

Behaviour during mating trials

According to the ranks of the aggressive scores from the above experiments, males and females were characterized as aggressive (top third), moderately aggressive (middle third) or nonaggressive (lower third), respectively. Male and female mean aggression scores differed significantly (see Results), hence we ranked the sexes separately. We placed a male on the web of a female ($N = 30$) (both were matched for their aggressive scores, i.e. assortatively mated by aggressiveness) and observed female aggressive behaviour towards the male as described above. For males, we recorded the total duration of courtship and the frequency of touching the females (interpreted as boldness towards a female mate). We observed spider behaviour for 20 min but left them together for the next 24 h to ensure successful mating.

Voracity towards prey and superfluous killing

In this test we gently placed a fly on the web 10 cm away from the female sitting in her retreat. We standardized female hunger level by starving the females for 3 days before the experiment. We measured the latency to the first movement and the latency to attack the prey. After the attack, a second fly was introduced to test for superfluous killing, as an evaluation of aggressiveness towards prey regardless of hunger. The superfluous killing trials follow the protocols developed by Riechert and Maupin to test for aggressiveness towards prey in several different web-building spider species (Riechert & Maupin 1998; Maupin & Riechert 2001). To assess food intake, we weighed the flies before the experiments and on the next day. We assumed mass loss due to desiccation to be similar among flies (median = 0.1068 g; quartile coefficient of dispersion = 7.5%) as flies were similar in size, and time and conditions between the two measurements were the same for all trials.

We did not succeed in measuring voracity towards prey if females had not built a complete web. This occurred in 30 females from the first generation and 112 females from the second generation. The second generation was tested for voracity towards prey at earlier age, when they inhabited the frame for less time, than the first one, which is probably the reason for the relatively lower percentage of fully built webs.

Body Measures and Reproductive Output

After the personality characterization, females and males were kept in their frames and cups, respectively, until they died a natural death. Dead spiders were stored in 70% alcohol and their patella + tibia I length, carapace length and width were measured to an accuracy of 0.01 mm.

Most of the females lived for 5 months after the experiments. During this time we checked each frame five times per week for deposited egg cases. All egg cases were then stored in a climate chamber at 25 °C until hatching. After the second moult, the spiderlings were separated into individual plastic cups (200 ml).

Heritability of Behaviours

Twenty-nine out of 30 females produced at least one egg case. Approximately 30 spiderlings from each pair were reared under standardized conditions as outlined above, until adulthood, when we tested five males and five females (per family, some clutches were very sex biased, thus in some cases we tested fewer than 10 spiders) for their behavioural trait values in the same way as the parental generation. We tested spiderlings ($N = 270$) for only those behavioural traits that were found to be repeatable in the parental generation (behaviours related to activity in novel environment, aggressiveness towards the same-sex conspecific, aggressiveness towards mates, voracity towards prey). We followed an approach described in (Riska et al. 1989), where the trait values (here behavioural traits) of F1 reared offspring are compared to the trait values shown by their wild-caught parents.

Mass Gain and Survivorship Under High-density Condition

In the last phase, we estimated mass gain from the beginning of the experiment and survivorship of spiders (whether the spiders died or not) kept in groups of 10 individuals. The groups were composed of individuals from either the same or different aggressiveness classes (all aggressive or all not aggressive) in an even ratio. Groups were housed in terraria (60 × 12 cm and 60 cm high) with a gradient in quality/prey density that was established by placing a single light source above one end of each terrarium (Fig. 1). Groups were provided with identical prey regimes (i.e. 1 g

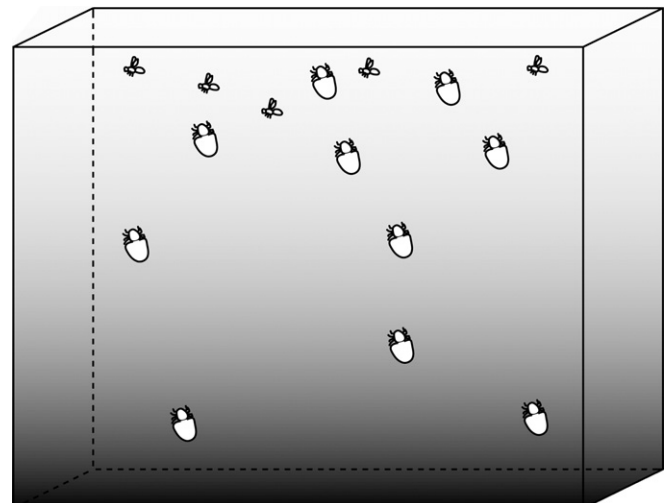


Figure 1. A frame (60 × 12 cm and 60 cm high) with a gradient in quality/prey density that was established by placing a single light source above one end of each terrarium. The groups were composed of 10 individuals from either the same or different aggressiveness classes (all aggressive or all not aggressive) in an even ratio. After 3 weeks we estimated mass gain from the beginning of the experiment and survivorship of spiders (whether the spiders died or not).

of flies twice per week). The flies were attracted by the light and accumulated in the brighter part of the terrarium. Such a set-up was created to mimic the 'field' conditions, in which spiders compete for preferred (light) sites. We had five replicates per treatment, resulting in 15 groups. During the experiment, spiders from one group escaped, and we discarded this group from the analysis. We used only mature spiders, which were offspring from assortatively mated parents. Parents were either from the upper or lower third of the distribution of aggression levels. After a period of 3 weeks, mortality and individual body mass were assessed.

Statistical Analyses

Effects of sex and generation on behavioural trait values were tested using a general linear model (LM).

Between-individual variability was analysed using the equation: $((Q75 - Q25)/(Q25 + Q75)) \times 100$, where $Q25$ = first quartile value and $Q75$ = third quartile value. The equation defines the quartile coefficient of dispersion, which is a descriptive statistic that measures dispersion (Das 2008). It is a relative measure used to make comparisons within and between data sets (Das 2008). Quartiles that are far apart relative to the absolute trait values are deemed to have greater dispersion. We defined behaviours with values above 50% as indicating significant differences between individuals.

Repeatability of behavioural values was analysed by repeatability tests (Falconer 1996). Length of patella + tibia I, carapace length and width values were subjected to principal component analysis (PCA). We used regressed factor scores for the body size measures. Probabilities of all correlations were adjusted with sequential Bonferroni corrections.

Heritability of behavioural traits was assessed using linear, mid-parent (i.e. the mean of the father's and mother's traits) on offspring regression (Roff 2002; e.g. Pruitt & Riechert 2009a). We used the mean offspring trait value for each family separated for sex (the mean of the five female and five male offspring) in this analysis. Heritability was estimated as the slope of the regression line (Boake 1994).

We compared mass gain and survivorship (dependent variables) between different high-density group classes (explanatory factors) using LMs. Where we found statistically significant difference between classes, we compared groups using post hoc tests with Bonferroni corrected alphas.

We compared the aggressiveness scores between *L. sclopetarius* and a highly sexually size dimorphic spider, *Nephilengys livida* (for details see Kralj-Fiser et al. 2012) using a Mann–Whitney *U* test.

Non-normally distributed data were $\log(x + 1)$ transformed for parametric statistics where needed. We performed all analyses using PASW 18 software (SPSS Inc., Chicago, IL, U.S.A.).

RESULTS

Effects of Sex and Generation

Sex and generation largely affected behavioural trait values (Table 1). In general, males showed more aggressive behaviour in the intra-sex contests than females (Fig. 2a). In comparison to their parents, spiders of the F1 generation were less active after placed in the novel environment, and male offspring were less aggressive towards same-sex conspecifics and offspring females towards mates, but offspring of both sexes were bolder after a simulated predatory attack (Table 1, Fig. 2a,b).

Table 1
LMMs tested for the effects of sex and/or generation (parental, offspring) on behavioural traits (BT) values

BTs	Factors	<i>F</i>	<i>P</i>	<i>df</i>
Duration of activity when placed in novel environment	sex	0.52	0.471	286.83
	generation	5.753	0.017	296.11
	sex*generation	3.161	<i>0.076</i>	286.9
Latency to regain activity in novel environment	sex	0.898	0.344	289.15
	generation	1.046	0.307	296.96
	sex*generation	1.923	0.167	289.26
Aggressiveness towards same sex (scores)	sex	85.29	>0.001	289.63
	generation	6.815	0.01	293.1
	sex*generation	0.342	0.559	289.92
Boldness (latency to recover after attack)	sex	1.790	0.179	285.97
	generation	66.132	>0.001	294.42
	sex*generation	8.829	0.003	286.1
Aggressiveness towards mate (scores)	sex	81.338	>0.001	135.56
	generation			
Voracity towards prey (latency to attack)	generation	2.231	0.138	116

Behavioural traits are dependent variables, sex and generation are fixed factors, random factors are female and male IDs (parental generation), and clutch IDs (offspring generation). Significant *P* values are indicated in bold, trends in italics.

Between-individual Variability

All measured variables except spider mass and levels of superfluous killing showed between-individual variability higher than 50% (Table 2).

Repeatability and Heritability of Behavioural Values

Aggressiveness towards a same-sex conspecific was highly repeatable in male and female spiders and was significantly heritable (Table 3, Fig. 2c). Similar results were found for boldness, although heritability of boldness appeared to be moderate and not significant (Table 3, Fig. 2d). Behaviours related to activity in the novel environment in both sexes as well as aggressiveness towards mates and voracity towards prey in females were significantly repeatable but not heritable behavioural traits (Table 3). Male behaviours during mating and female superfluous killing were not repeatable (Table 3).

Behavioural Correlations

The only correlation consistent in both generations was found between the two measured behaviours in the novel environment. The longer the spiders moved in the novel environment after being placed in an unfamiliar box, the shorter the duration to the next activity (Table 4). In females from the offspring generation, this activity positively correlated with voracity towards prey (Table 4) and in parental behaviour in an unfamiliar box and boldness after a simulated predator attack were correlated (Table 4).

Behavioural Correlations with Body Mass, Size and Reproductive Output in Parental Generation

In females from the offspring generation, mass positively correlated with voracity towards prey, and behaviours related to activity in a novel environment (Table 4), but all other behavioural traits were independent from spider mass and size (Table 4). There was no correlation between any of the behavioural traits and the number of egg cases deposited by females (duration of locomotor activity in novel environment: $P = 0.237$; latency to regained activity in novel environment: $P = 0.121$; intra-sex aggression: $P = 0.368$; boldness: $P = 0.319$; aggression towards mate: $P = 0.69$; voracity towards prey: $P = 0.772$).

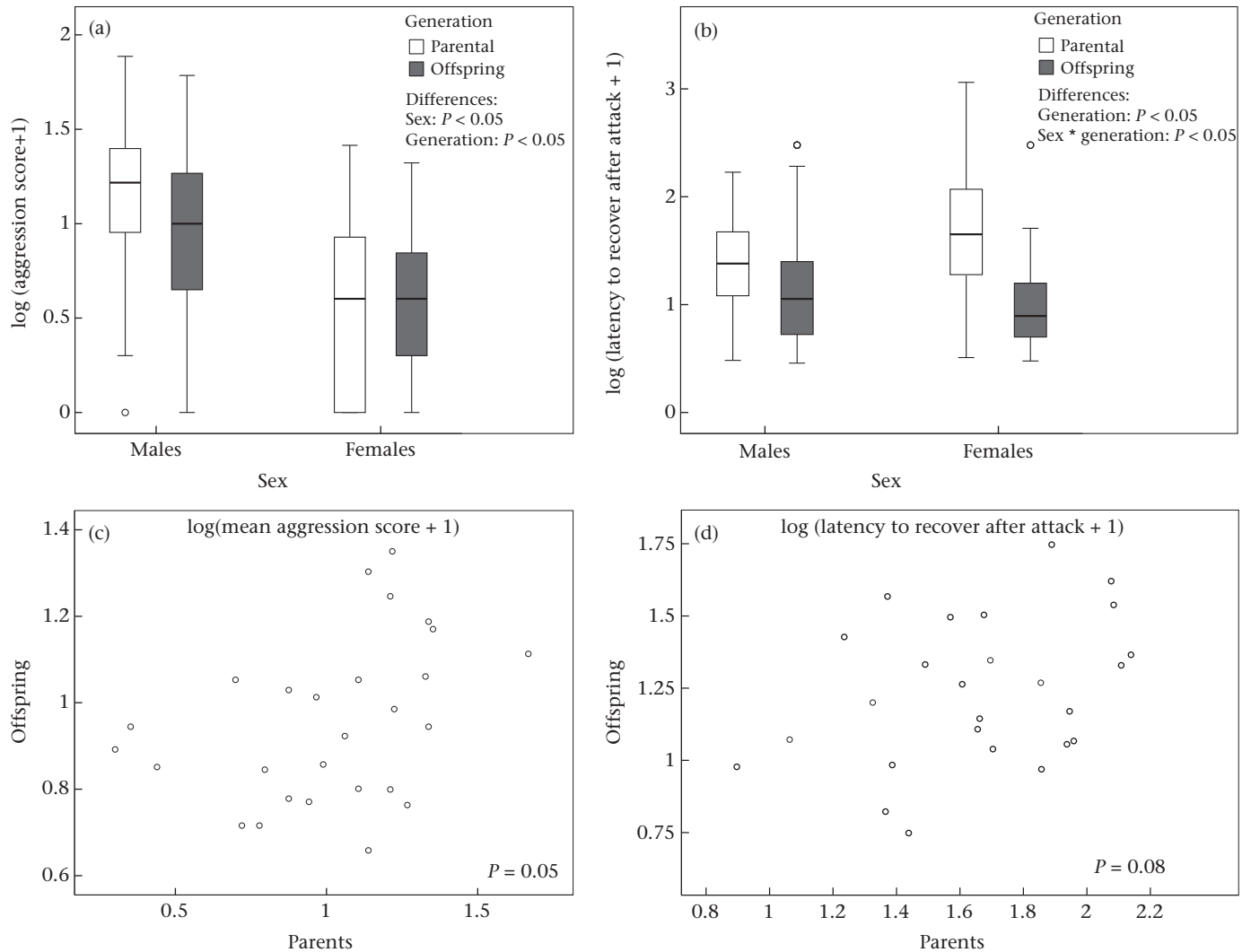


Figure 2. (a) Differences in aggression scores in intra-sex contests. (b) Differences in boldness after simulated predator attack. (c) Heritability of aggressiveness in intra-sex contests assessed by linear, mid-parent (i.e. the mean of the father and mother traits) on mid-offspring regression (10 siblings: five males, five females). (d) Heritability of boldness assessed by linear, mid-parent (i.e. the mean of the father and mother traits) on offspring regression (10 siblings: five males, five females). The box plots show the median and 25th and 75th percentiles; the whiskers indicate the values within 1.5 times the interquartile range and the circles are the outliers.

Comparison of Aggression Intensity Between *L. sclopetarius* and *N. livida*

Males of *L. sclopetarius* ($N = 31$) were significantly more aggressive during male–male contests than were *N. livida* males

($N = 22$) ($U = 207.5$, $P = 0.016$). Females of the two species, however, did not significantly differ in aggressiveness intensity during female–female contests ($U = 275$, $P = 0.844$), but showed different between-individual variability in aggressiveness (*L. sclopetarius*: 100%, $Q_{25} = 0$, $Q_{75} = 7.25$; *N. livida* 75%, $Q_{25} = 1$, $Q_{75} = 7$).

Table 2

Between-individual variability in mass and behaviour

	Males	Females
Weight (g)	14.27	26.57
Locomotor activity in NE (s)	52.52	53.01
Regained activity in NE (s)	61.91	64.57
Boldness (s)	62.83	73.61
Aggression towards conspecific (score)	52.38	100.00
Aggression towards mate (score)	/	84.42
Voracity towards prey (s)	/	67.39
Superfluous killing (% leftovers)	/	38.43
Court to female (s)	100.00	/
Touch female (N)	100.00	/

NE: novel environment. We analysed the between-individual variability using the equation: $((Q_{75} - Q_{25}) / (Q_{25} + Q_{75})) \times 100$, where Q_{25} = first quartile value and Q_{75} = third quartile value. We determined the behaviours with values higher than 50% to be considerably variable between individuals (marked in bold).

Mass Gain and Survivorship in High-density Groups

The composition of mean aggressiveness in high-density groups significantly affected mean body mass after 3 weeks ($F_{2,12} = 4.625$, $P = 0.035$; Fig. 3a) such that mean individual body mass was higher in the aggressive groups than in the mixed groups (post hoc with Bonferroni correction, $P = 0.034$). This was an effect of the treatment, as the groups did not vary in individual mass at the beginning of the experiment ($F_{2,12} = 1.008$, $P = 0.396$). There was a nonsignificant trend towards a higher mortality rate in the aggressive than in the mixed groups ($F_{2,12} = 3.466$, $P = 0.068$; Fig. 3b; post hoc with Bonferroni correction, $P = 0.082$). Aggressive, nonaggressive and mixed groups did not differ in their reproductive output (total number of egg cases: $F_{2,12} = 0.024$, $P = 0.976$, total mass of egg

Table 3
Results of behavioural repeatability and heritability

		Repeatability		Heritability
		Fathers (N=30)	Mothers (N=31)	Offspring (N=270)
Duration of activity when placed NE	R	0.894	<i>0.401</i>	0.107
	P	<0.001	<i>0.087</i>	0.602
Latency to regain activity in NE	R	0.734	0.53	0.038
	P	<0.001	0.023	0.851
Boldness	R	0.798	0.824	0.35
	P	<0.001	<0.001	0.08
Aggression towards same-sex conspecific	R	0.864	0.772	0.381
	P	<0.001	<0.001	0.05
Aggression towards mate	R	na	0.573	0.025
	P	na	0.014	0.9
Voracity towards prey	R	na	0.632	0.121
	P	na	0.005	0.547
Superfluous killing	R	na	0.142	na
	P	na	0.615	na
Courtship duration	R	0.006	na	na
	P	0.506	na	na
Boldness towards female	R	0.28	na	na
	P	0.183	na	na

na: not applicable; NE: novel environment. Significant *P* values are indicated in bold, trends in italics.

cases: $F_{2,12} = 0.731$, $P = 0.504$; mean individual mass of egg cases: $F_{2,12} = 0.053$, $P = 0.949$).

DISCUSSION

The results of our study lend support to both our hypotheses, as *L. sclopetarius* exhibit both personality polymorphism and behavioural plasticity. Individual differences in *L. sclopetarius* intra-sex aggression levels appeared to be heritable and may thus possess an additive genetic component (van Oers et al. 2005; Pruitt et al. 2010). Similarly, boldness was repeatable and tended to be a heritable trait. However, *L. sclopetarius* spiders behaved much bolder in the predatory test than other spiders tested in similar test conditions (Pruitt et al. 2008; Kralj-Fišer, unpublished). We argue that increased boldness might be advantageous in urban environments, because urban environments may contain fewer enemies (e.g. predators; Shochat et al. 2006). Furthermore, the results of examining spider fitness under high-density conditions provided no

clear-cut results. The differences that appeared after only 3 weeks may suggest that not only groups of tolerant spiders but also a balanced mix of aggressive and tolerant individuals allows successful coexistence at high density, whereas a group consisting of aggressive individuals is more likely to exclude each other either through cannibalism or through starvation. Further experiments with stronger and varying competitive regimes are required to verify our preliminary notion that a mix of aggressive types probably eases life in aggregations and hence promotes success as an urban dweller (e.g. Pruitt & Riechert 2009b, 2011; Fogarty et al. 2011).

Polymorphism in a population can be maintained in two ways: each individual can play actions randomly with fixed probabilities and thus produce the predicted mix of strategies in populations, or fixed proportions of individuals can perform each strategy consistently (Dall et al. 2004). The latter scenario, which generates heritable personality differences, may apply to *L. sclopetarius*, if survival in high-density groups does indeed depend on the relative frequencies of aggressive and tolerant behavioural types (Dall et al. 2004; Sih et al. 2004; Wolf et al. 2007, Wolf & Weissing 2010; Dubois et al. 2010; but see Kurvers et al. 2011). Similar dynamics were found in the social spider *Anelosimus studiosus*, in which both social and asocial females experience fitness benefits in terms of relative egg sac mass in the presence of unlike individuals (Pruitt et al. 2011).

One of the possible explanations for success of *L. sclopetarius* was high individual behavioural plasticity, and/or reduction of intraspecific aggression on a population level. In contrast to this prediction, wild-caught and laboratory-tested adult *L. sclopetarius* showed significant between-individual variation and low within-individual variation in aggression between the same sex, female voracity towards prey, behaviour in novel environment and boldness, which is in accordance with other personality studies on invertebrates and vertebrates (Gosling 2001; Sih et al. 2004; Bell et al. 2009; Pruitt et al. 2010). Hence, even though this urban species had to adapt to changes in the environment, behaviour of adult individuals is rather canalized and probably encompasses a low individual behavioural reaction norm (Dingemans et al. 2010). Furthermore, a comparison between females of *L. sclopetarius* and *N. livida*, an orb-weaver from disturbed and natural environments, revealed that females of the two species did not show significantly different levels of intraspecific aggression in same-sex contests (this study; Kralj-Fišer et al. 2012). Hence, our data are at

Table 4
Probabilities of Pearson correlations separated for different generations and sexes

	Generation	Locomotor activity in NE		Regained activity in NE		Intra-sex aggressiveness		Boldness		Aggression towards mate		Voracity towards prey	
		Parent	Offspring	Parent	Offspring	Parent	Offspring	Parent	Offspring	Parent	Offspring	Parent	Offspring
Females	Mass	0.924	0.02	0.412	0.001*	0.503	0.517	0.832	0.566	0.892	0.699	0.952	0.038
	Boldness	0.099	0.623	0.039*	0.958	0.404	0.536	/	/	0.211	0.28	0.026	0.321
	Intra-sex aggressiveness	0.25	0.448	0.124	0.946	/	/	/	/	0.883	0.538	0.328	0.853
	Locomotor activity in NE	/	/	/	/	/	/	/	/	0.585	0.649	0.234	0.284
	Regained activity in NE	0.243	0.004*	/	/	/	/	/	/	0.052	0.209	0.799	0.019*
	Size	0.194	na	0.627	na	0.472	na	0.531	na	0.824	na	0.837	na
	Aggression towards mate	/	/	/	/	/	/	/	/	/	/	0.918	0.824
	Males	Mass	0.155	0.028	0.303	0.281	0.259	0.381	0.108	0.931	na	na	na
Boldness	0.111	0.113	0.568	0.46	0.796	0.748	na	na	na	na	na	na	
Intra-sex aggressiveness	0.955	0.932	0.909	0.882	/	/	na	na	na	na	na	na	
Regained act. in NE	0.014*	<0.001*	/	/	/	/	na	na	na	na	na	na	
Size	0.028	na	0.281	na	0.381	na	0.931	na	na	na	na	na	

na: not applicable; NE: novel environment. Significant probabilities after Bonferroni correction are marked with an asterisk.

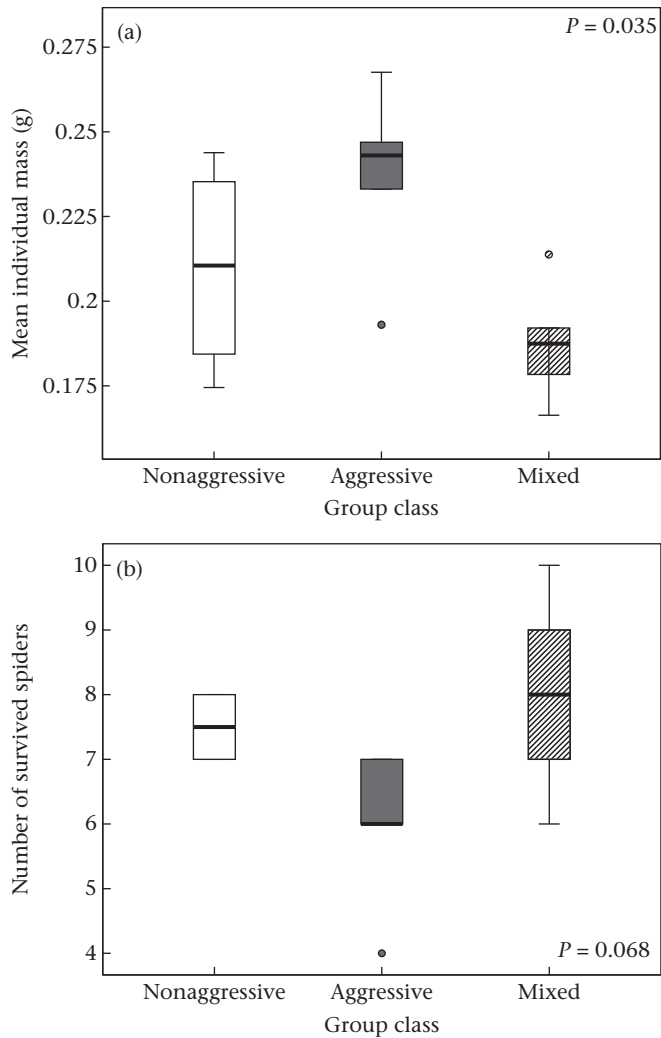


Figure 3. (a) Differences in the mean individual mass after 3 weeks in high-density conditions. (b) Differences in the number of survived individuals after 3 weeks in high-density conditions. The box plots show the median and 25th and 75th percentiles; the whiskers indicate the values within 1.5 times the interquartile range and the circles are the outliers.

odds with the long-standing hypothesis that adaptation to an urban environment and high-density (colonial) living requires a reduction in aggressiveness among female conspecifics (Riechert 1985; Hodge & Uetz 1995). Yet, *L. sclopetarius* females showed higher between-individual variability in aggressiveness than *N. livida*, supporting the hypothesis that aggressiveness personality polymorphism, not a lower average intraspecific aggressiveness, is present in *L. sclopetarius* and may be advantageous in the successful establishment of high-density populations (e.g. Fogarty et al. 2011; Pruitt & Riechert 2011). Still, the above interspecific differences and similarities might have resulted from other factors, such as ecological and phylogenetic parameters; hence comparison with higher number of (related) species is needed.

Similarly to aggression, boldness seems to be a universal trait found in a number of species (Wilson et al. 1994; van Oers et al. 2005; Pruitt et al. 2010). *Larinioides sclopetarius* exhibited higher boldness compared with other species of spiders, and this may have played a role in its success in urban environments. Boldness in spiders is generally measured by the time the spider spends motionless after being exposed to a novel situation. For example,

Anelosimus studiosus and *Nuctenea umbratica* freeze or feign death within seconds after being placed into a new container (Pruitt et al. 2008; Kralj-Fišer, unpublished). By contrast, *L. sclopetarius* placed into a novel container almost never feigned death, but only did so after the container was shaken for several minutes. High boldness might correspond with high feeding activity and quick acclimatization to a novel environment (Wilson et al. 1994; Møller 2010), both being favoured in urban environments, where nocturnal spiders have few predators (see also Dingemanse et al. 2007; Bell & Sih 2007), and thus deserve further attention.

In contrast to results derived from many vertebrate species (van Oers et al. 2005) and the only spider species previously analysed for heritability of behavioural traits (*A. studiosus*; Pruitt & Riechert 2009a), behaviours related to activity in novel environment and voracity towards prey were not heritable in *L. sclopetarius*. This suggests that the expression of these behaviours is largely shaped by the environment. Our results may imply that behaviour in novel environment and voracity towards prey in *L. sclopetarius* share high plasticity (i.e. the extent to which behaviour expressed by individuals within a given genotype varies as a function of the set of conditions experienced by those individuals before the behaviour was expressed; Stamps & Groothuis 2010; Schuett et al. 2011). In fact, plasticity in these behaviours corresponds to high plasticity in growth patterns depending on food availability in *L. sclopetarius*, both allowing these species to thrive in the cities (Kleinteich & Schneider 2010).

Personality traits are commonly intercorrelated (Sih et al. 2004). However, several studies unravelled 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, 2009; Bell & Sih 2007; Stamps & Groothuis 2010). In our study, where individuals show stability in behavioural traits, but no correlations between them, (Dingemanse et al. 2007, 2009; Bell & Sih 2007), we assume that behaviour in novel environment and voracity towards prey are plastic during *L. sclopetarius* development; hence, the lack of correlations between these traits in the wild-caught generation might be explained by developmental plasticity. The same mechanism may then explain the differences in correlations between the two generations.

In conclusion, the urban spider species *L. sclopetarius* shows high between- and low intra-individual variability in behaviour. In accordance with findings from a number of species, *L. sclopetarius* aggressiveness levels and boldness seem to possess additive genetic components. We suggest negative frequency-dependent selection as a candidate mechanism to generate genetic polymorphism for aggressiveness and boldness (at the population level). A balanced mix of aggressive and tolerant individuals may facilitate *L. sclopetarius* populations in spreading and establishing high abundances in urban environments. Low heritability of behaviours related to foraging success and a lack of behavioural correlations suggest that developmental plasticity might be another mechanism that promotes success in novel city environments.

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