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ORIGINAL ARTICLE

Different patterns of behavioral variation across and within species of spiders with differing degrees of urbanization

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Abstract
Behavioral characteristics importantly shape an animals' ability to adapt to changing conditions. The notion that behavioral flexibility facilitates exploitation of urban environments has received mixed support, but recent studies propose that between-individual differences are important. We leverage existing knowledge on three species of orb-web spider (Araneidae, Araneae) whose abundances differ along an urban–rural gradient to test predictions about between- and within-species/individual behavioral variation. We sampled *Larinioides sclopetarius* from their urban environment, and two species from suburban environments, *Zygiella x-notata* and *Nuctenea umbratica*. For each species, we quantified activity in a novel environment and within-species aggression. We analyzed between- and within-individual variation in behavior as well as their repeatability and correlations. As predicted, *L. sclopetarius* exhibited the highest activity in a novel environment and *N. umbratica* the lowest. Across all species, males were more aggressive than females and *Z. x-notata* was the most aggressive, followed by *L. sclopetarius* and *N. umbratica.* For all species, between-individual differences in activity and aggressiveness were repeatable; but the two behaviors were not correlated for any species. We next tested how group composition in relation to aggressiveness affects survival in high density conditions. Groups of *Z. x-notata* consisting of aggressive and tolerant spiders had higher survival rates than groups composed of only aggressive or tolerant individuals. Ultimately, we uncovered a complex pattern of behavioral variation between species as well as between and within individuals and we discuss the relative roles of this variation with respect to adapting to urban environments.

Significance statement
Urbanization has drastically changed biodiversity patterns. While the majority of species cope poorly with urban habitats, some species flourish in cities. Our understanding of behavioral characteristics that facilitate this exploitation, however, remains poor. We explored between and within species and individual variation in behaviors in ecologically similar orb-weaving spider species whose abundances differ along the urban–rural gradient. We detect both consistent individual differences and plasticity, in individuals' response to a novel environment, suggesting that some degree of flexibility in reaction to novelty may be crucial in an urbanized environment. We also found that variation in aggressiveness type enables survival in high density conditions, conditions typical for urban populations. Urban populations thus exhibit a complex pattern of behavioral flexibility and behavioral stability.

Keywords Personality · Urbanization · Repeatability · Behavioral types · Group composition

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Introduction

Behavior plays an important role in an animal's ability to deal with changes in its environment, including human-induced changes (Shochat et al. 2006; Sih et al. 2010; Tuomainen and Candolin 2011). While the vast majority of species appear to cope poorly with highly urbanized environments, certain species (e.g., fire ants, pigeons, rats) flourish in cities (Kark et al. 2007; Sol et al. 2013) where they can reach extraordinarily high abundances in city cores (McKinney 2002, 2006). The life histories of these "urban exploiters" are often characterized by rapid proliferation, and a number of studies have begun to explore associated behavioral characteristics that might facilitate urban exploitation. To date, behavior of urban dwelling species has been explored at predominantly three distinct scales—(i) across-species/population behavior (inter-species/population variation); (ii) within-species, between-individual behavior (between-individual variation); and (iii) within-species, within-individual behavior (within-individual variation).

Across different taxonomic groups, successful urban species have been shown to exhibit reduced escape behavior, higher aggression, and faster exploitation of novel resources as compared to non-rural relatives (freshwater turtles: *Trachemys scripta elegans* vs. *Mauremys leprosa*, Polo-Cavia et al. 2008; vultures: *Coragyps atratus* vs. *Vultur gryphus*, Carrete et al. 2010; several bird species, Sol et al. 2012, 2013). Similarly, within-species studies that compared conspecifics from rural vs. urban populations revealed that individuals from urban populations tend to be more active and to exhibit more (albeit superficial) exploration, reduced escape responses, increased risk-taking behavior, and more aggression (eastern gray squirrel, *Sciurus carolinensis*, Partan et al. 2010; noisy miner, *Manorina melanocephala*, Lowry et al. 2011; song sparrows, *Melospiza melodia*, Scales et al. 2011; Cape ground squirrel, *Xerus inauris*, Chapman et al. 2012; 15 bird species, Møller and Ibáñez-Álamo 2012; reviewed in Miranda et al. 2013). Additionally, a comparison of 20 bird species invading rural and urban habitats found that birds from urban environments tended to have a greater between-individual variation in a proxy of escape behavior (i.e., flight initiation distance) than their rural conspecifics (Carrete and Tella 2011). These results and further studies corroborate the view that variation among individuals in behavior traits may help explain a population's ability to adapt to urban environments (Sih et al. 2004, 2010; reviewed in Miranda et al. 2013).

Between-individual variation in behavior traits is increasingly being studied to explain a population's ability to adapt to urban environments (Evans et al. 2010; Carrete and Tella 2011; Scales et al. 2011; Atwell et al. 2012; Bókony et al. 2012; Carrete and Tella 2013; reviewed in Miranda et al. 2013). The co-existence of different behavioral types, in particular, may allow coping with a broad range of environmental conditions, e.g., exploitation of diverse resources and niches in urban environments (Møller 2010; Sih et al. 2010, 2012; Kralj-Fišer and Schneider 2012; Sih 2013). Furthermore, increased between-individual variation in behavior is expected to result in higher functional diversity of species, e.g., aggressive individuals may be good initial dispersers, whereas socially tolerant individuals may cause population proliferation (Fogarty et al. 2011; Sih et al. 2012). On the other hand, constraints in behavioral expression within individuals may be disadvantageous in unpredictable urban environments. Interestingly, several studies that compared rural and urban populations found that these differed in architecture of their behavioral types; namely, rural individuals tended to exhibit tighter correlations among behavior traits (e.g., behavioral syndromes) as compared to urban conspecifics (Evans et al. 2010; Scales et al. 2011; Bókony et al. 2012; Miranda et al. 2013). This implies that the association between behavioral traits may be more flexible in urban compared to rural species or populations and potentially less constraining.

Despite a growing body of research examining the relationship between behavioral traits and success at adapting to and colonizing urban environments, the relationship remains unclear. While a certain degree of within-individual variability (e.g., behavioral plasticity) is crucial to cope with unpredictable/novel environments (Sol et al. 2013; Wong and Candolin 2015), the same plasticity may also be maladaptive (Sinervo et al. 2010; Robertson et al. 2013; Wong and Candolin 2015). Costs of plasticity may be "evaded" through behavioral streamlining, because different (stable) behavioral types may do equally well when exposed to a range of (spatially and temporary) different contexts (Watters and Sih 2005; Cote et al. 2010; Sih et al. 2010; Fogarty et al. 2011; Wolf and Weissing 2012). On the other hand, constraints in behavioral responsiveness to environmental change would likely reduce an individuals' ability to cope with urban environments. Thus, the spread and maintenance of urban populations likely involve a complex dynamic of between- and within-individual variation in behavioral traits (Kralj-Fišer and Schneider 2012; Sol et al. 2013; Halpin and Johnson 2014).

To date, behavioral characteristics of urban dwellers have been mainly studied in birds and mammals (e.g., Evans et al. 2010; Møller 2010; Partan et al. 2010; Atwell et al. 2012; Bókony et al. 2012; Bateman and Fleming 2014). Surprisingly, arthropods remain largely underexplored in this respect (but see Halpin and Johnson 2014), yet they represent providers of important ecosystem services such as decomposition, pollination, food web interactions, and biological control (Kotze et al. 2011). Additionally, due to their abundance and short generation time, arthropods are good models to study behavioral responses to urbanization (McIntyre 2000; Niemelä and Kotze 2009; Kotze et al. 2011; Kralj-Fišer and Schuett 2014). Arthropods also contain the archetypical urban pests such as cockroaches, fleas, bed bugs, and others whose spreading is medically and economically important.

Among arthropods, orb-weaving spiders (Araneae, Araneoidea) make particularly suitable organisms to study characteristics of urban dwellers. Urbanized environments provide web-building spiders' ample opportunities for building webs, and artificial light likely increases their foraging success by attracting insects (Heiling 1999). City-dwelling prey may also be available for an extended period in the season due to favorable urban temperatures (Heiling 1999; Kotze et al. 2011), potentially increasing the spiders' reproductive season and time to produce offspring. Indeed, a combination of increased food availability and decreased predator exposure may translate to higher fecundity, survival, and reproductive output, as has been shown in the Australian golden orb weaver *Nephila plumipes* (Lowe et al. 2014). However, other studies found decreased reproductive rate and fecundity in individuals inhabiting urban environments in *Nephila clavata* (Miyashita 1990) and in widow spiders *Latrodectus hesperus* (Johnson et al. 2012), respectively, implying that only certain spider species may adapt well to urban environments.

Here, we explore behavioral traits in three distinct species of orb-weaving spiders (Family Araneidae) that each tends to inhabit environments characteristic of different levels of urbanization with varying success. *Larinioides sclopetarius* represents a strictly urban species (i.e., urban exploiter) (Kleinteich 2010; Kleinteich and Schneider 2011), whereas *Z. x-notata* and *N. umbratica* inhabit both urban and more pristine environments (Leborgne and Pasquet 1987; Bucher and Entling 2011). Prior laboratory studies aimed to understand why the three species differ in their success as city dwellers found that *L. sclopetarius* exhibit high developmental plasticity depending on food availability (e.g., growth rate, number of instars), a short life cycle (60 days at ample food), and high reproductive output (up to 12 viable egg cases, Kleinteich and Schneider 2011, our unpublished data). *Zygiella x-notata* exhibits developmental plasticity (growth rate, number of instars) and has intermediate developmental time (160 days at ample food, Mayntz et al. 2003) and reproductive output (up to eight viable egg cases, our unpublished data). Finally, *N. umbratica* showed a rather canalized development, a long life cycle (240 days at ample food, Kralj-Fišer et al. 2014), and comparably lower reproductive output (up to four viable egg cases, our unpublished data). We suspect that the combination of high food availability in urban environment and associated increased growth through developmental plasticity and short generation times facilitate the successful exploitation of urban environments by *L. sclopetarius* and *Z. x-notata.* We also hypothesize that differences in behavior exist both between and within species.

We aimed to quantify and compare behavioral characteristics of three species of spider that vary in their successful establishment in urban envrionments. Specifically, we use between-species and within-species comparisons of *L. sclopetarius*, *Z. x-notata*, and *N. umbratica* to examine (i) exploration of novel environments and (ii) aggression levels with same-sex conspecifics. We assessed the relative contribution of behavioral constancy and behavioral plasticity in individuals' traits. We analyzed repeatability; i.e., proportion of phenotypic variation (amount of within-individual variance) in a trait relative to the total phenotypic variation (sum of within- and between-individual variance). Furthermore, we examined potential individual differences in behavioral plasticity in response to repeated novel environment test using reaction norm approach (Dingemanse and Dochtermann 2013). Next, we examine the relationship between aggression and high density living as it relates to survival. We do this by using our calculations of aggression to artificially create high density populations of *N. umbratica* and *Z. x-notata* (data already exists on *L. sclopetarius*, Kralj-Fišer and Schneider 2012) whose composition consists of different behavioral types, and we assess individual survival over time.

Given that a bold response to novelty has been repeatedly shown as a key behavior determining animals' ability to dwell in urban habitats (reviewed in Miranda et al. 2013), we predicted *L. sclopetarius*—our most successful urban species—would express the highest activity levels. Concerning within-species aggressiveness, we similarly expected higher levels of tolerance towards conspecifics in *L. sclopetarius* and *Z. x-notata*—the two species that naturally occur in aggregations—compared to "more solitary" *N. umbratica* (e.g., Holway 1998).

In terms of the relationship between the composition of aggressive individuals in high density populations and individuals' survival, prior work in *L. sclopetarius* found that groups consisting of a balanced mix of aggressive and tolerant individuals increased group survival (Kralj-Fišer and Schneider 2012). Similar results, where groups composed of individuals of mixed behavioral types outperformed monotypic groups, have been repeatedly found across diverse taxa (Dyer et al. 2009; Cote et al. 2010; Modlmeier et al. 2012; Pruitt et al. 2012; Keiser et al. 2014; Farine et al. 2015; Lichtenstein et al. 2016). As such, we expect that groups of mixed aggression levels in both *N. umbratica* and *Z. x-notata* will similarly experience the highest survival rates.

Methods

Study animals

Larinioides sclopetarius, commonly called the "bridge spider," can be found across the Holarctic and is an extremely successful colonizer of urban areas. High density populations, which may count up to 100 individuals per m^2 (Burgess and Uetz 1982; Heiling and Herberstein 1998; Schmitt 2004; Schmitt and Nioduschewski 2007a, 2007b), tend to colonize human urban constructions near bodies of water (Heiling and

Herberstein 1998). These nocturnal spiders often build webs adjacent to one another, but each web retains its full functionality (Heiling and Herberstein 1998). In areas inhabited by bridge spiders, few other orb weawers can be found; they are either entirely absent or limited to sporadic patches with low population densities (Kleinteich 2010).

Zygiella x-notata, also distributed across the Holarctic, is another successful colonizer of urban areas. This species can be found on human constructions such as walls, fences, and window frames, where they may be found in aggregations of up to 25 individuals per m^2 (estimated from results of Leborgne and Pasquet 1987). When found in the same habitat as *L. sclopetarius*, however, *L. sclopetarius* dominates and appears to outcompete *Z. x-notata* (Kleinteich 2010). In contrast to *L. sclopetarius*, *Z. x-notata* can be found on urban vegetation (e.g., hedges, parks), on trees, and on rocks in more pristine environments (Leborgne and Pasquet 1987; Heiling and Herberstein 1998).

Nuctenea umbratica is a widespread central European species. It is a habitat generalist that occurs in urban and pristine environments. Individuals of *N. umbratica* appear to prefer landscapes with semi-open habitats, such as forest edge, hedgerows, orchards, and single trees (Horváth and Szinetár 2002; Horváth et al. 2005; Bucher et al. 2010). When found in urban environments *Nuctenea* spiders inhabit trees, shrubs, or wooden constructions, where they build large orb webs. In cities, *N. umbratica* often co-occurs with, and is outcompeted by, *L. sclopetarius* and/or *Z. x-notata* (pers. obs.). Despite the fact that these spiders are ubiquitous (Horváth et al. 2005), we never observed them in large aggregations.

Species collections

We collected subadult *L. sclopetarius* males and females from artificial constructions, e.g., buildings, fences, and bridges, along riverbanks in two different locations in Hamburg, Germany (53.577401, 10.009699), in September 2010. We collected *Z. x-notata* subadults in May 2012 in suburban areas of Vipava from man-made constructions along the Vipava riverbank (all spiders were collected in one location), Slovenia (45.844605, 13.963604). We collected subadult *N. umbratica* spiders from their webs on trees and hedgerows along the Ljubljanica riverbank in suburban areas of Ljubljana (all spiders were collected in one location), Slovenia (46.045093, 14.506048), between May and July 2011. While *Z. x-notata* and *N. umbratica* were observed in rural, suburban, and urban environments, *L. sclopetarius* appeared only in urban areas. The density of individuals was the highest in *L. sclopetarius*, intermediate in *Z. x-notata*, and the lowest in *N. umbratica*.

Field-collected subadults of all three species were transferred to the closest laboratory (Germany, Slovenia), kept in 200-ml plastic cups, and fed with fruit flies (*Drosophila* sp.). Individuals were collected as subadults and then reared to adulthood in the laboratory to assure their virginity and thus the same mating status. Upon maturation, adult females, which are larger than males across all species, were transferred into plastic frames (36 × 36 × 6 cm) and fed with blowflies (*Calliphora* sp.) The adult males of all species cease web building upon sexual maturation, and were thus retained in plastic cups with feeding treatment as in females. Throughout the study, the spiders were kept at room temperature under LD 10:14 conditions, fed two flies twice a week, and water-sprayed 5 days a week. At maturity, we weighed all spiders (accuracy 0.01 mg) before subjecting them to experiments.

Experimental design

1. *Between and within-species behavioral variation*

We subjected spiders of all three focal species to two tests for behavioral characterization: (i) a novel environment test which measured behavior related to activity in a novel environment (duration of initial activity when placed into the novel environment); and (ii) a contest test which we used as a proxy for aggressiveness towards a same-sex conspecific. Using a repeated measures design in which each spider participated in both tests twice, we observed 61 *L. sclopetarius*, 61 *Z. x-notata*, and 85 *N. umbratica* individuals. We additionally repeatedly tested 10 additional *N. umbratica* spiders in the novel environment test. The order of tests and of observed individuals was chosen randomly. Though we aimed to test all individuals twice in each of the test situations, this was not always feasible due to death (*Z. x-notata*, $N = 3$; *N. umbratica*, $N = 3$). The spiders were always fed 1 day before testing, and an individual was never observed more than once a day. Unfortunately, it was not possible to record data blind because our study involved observations of focal animals.

2. *Activity in a novel environment*

In order to quantify each spider's activity level in a novel environment, we carefully placed a test spider into an unfamiliar plastic container (11 × 11 × 6 cm) 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 (hereafter termed duration of initial activity in a novel environment; e.g., Kralj-Fišer and Schneider 2012).

3. *Aggressiveness towards same-sex conspecific*

To calculate an individual's level of aggression with a same-sex conspecific, we staged two individuals about 5 cm from each other and recorded agonistic behavior for 20 min. Females were tested twice in random order with 1 to 3 weeks in between—once as residents in their own web and once as intruders on an unfamiliar web. Females usually reside in a retreat within a corner of the web frame. For female–female interactions then, an "intruder" female was gently placed into the resident web with a paintbrush. Male orb weavers cease web building after maturity. Thus, to observe male intra-sexual aggressiveness, two males were placed at the hub of a female web, approximately 5 cm from each other, while the female was in her retreat. Males and females were tested twice. No individual was paired with the same opponent more than once.

Aggressiveness was measured as a score based on the frequency of what we deem to be "aggressive" behavior: approaching (score = 1), web-shaking (score = 1), attacking (score = 2), and chasing (score = 3) (e.g., Kralj-Fišer et al. 2011; Kralj-Fišer and Schneider 2012). Aggressive behaviors were similar for all three species. "Approach" was defined as a movement by one spider towards the other individual, "web-shaking" was defined as sudden and large amplitude shaking of the web, which spiders usually exhibit when approaching another individual (Lubin 1980), "attacking" is defined as a sudden move in the direction of the other individual resulting in a body contact with the opponent, and "chasing" is defined as a running after the (escaping) opponent resulting in a successful attack or escape of the opponent. The sum of these scores for each individual was used as its aggressiveness score.

Statistical analyses

We first tested for inter-species differences in the behavioral scores using a generalized estimating equation (GEE) which allows for non-normal distribution and the repeated measures (subject = id, within = sequence). We assessed sex and species differences (independent variables) for each of the measured behaviors (dependent variables: activity scores, aggressiveness scores). We compared species and sexes using Wald chi-square statistics with least significant difference adjustments correcting for multiple comparisons, where appropriate. We performed these analyses in SPSS. We also performed Markov Chain Monte Carlo Linear Mixed Model (MCMCglmm) analyses in R (version 2.15.3, Core R Team 2013) with sex and species as independent factors (Hadfield 2010); Supplement 1 has R scripts and results. In the next step, we analyzed between- and within-individual variance of behaviors for each species separately (intra-species behavioral variation). To test for the existence of distinct behavioral variation in activity level and aggressiveness, we used the mixed-effect modeling approach (Dingemanse and Dochtermann 2013). We primarily estimated the degree to which the trait expression varies among individuals (between-individual variance) and the degree to which the trait expression varies within an individual (within-individual variance), which we also used to calculate repeatability. High between-individual variance vs. low within-individual variance in a trait expression implies the existence of stable individual differences in the trait while the within-individual variance informs on average plasticity in the expressed behavior.

We used the Markov Chain Monte Carlo Linear Mixed Model (MCMCglmm) to estimate the sources of variation in behavioral measures (dependent variables) and to analyze the behavioral correlations (Dingemanse and Dochtermann 2013) for each species separately. We performed these analyses in R (version 2.15.3, Core R Team 2013) using the MCMCglmm package (Hadfield 2010).

In order to decompose phenotypic variance to within- and between-individual components, we included individual as random effect in the model. To estimate the significance of between-individual variance in intercept or elevation, we compared the deviance information criterion (DIC) (Grueber et al. 2011) of constrained (without random factor) and unconstrained models (id as random factor), and assumed better fit of the model when DIC constrained − DIC unconstrained >5. We added sex and test sequence as fixed effects in the model and calculated the adjusted repeatability with 95% confidence interval according to Nakagawa and Schielzeth (2010). We applied Box-Cox to transform data of initial activity in a novel environment (Box and Cox 1964; Osborne 2010) using MASS (Ripley et al. 2011). Scripts are given in Supplement 2.

We used bivariate mix-effects modeling to assess behavioral correlations. We calculated phenotypic correlations between aggressiveness and initial activity following the approach suggested by Dingemanse and Dochtermann (2013). We also partitioned out the between-individual correlations from the phenotypic ones because a between-individual correlation need not be captured effectively by the phenotypic correlation; estimating the between-individual correlation has been advised to be used in behavioral syndrome research (Dingemanse and Dochtermann 2013). We compared DIC of constrained (inter- and within-individual co-variances are set to zero) and unconstrained models (within-individual co-variance is set to zero) for a better fit. Both variables were transformed with log function, because models with data being Box-Cox transformed appeared unstable. Scripts are given in Supplement 3.

In the above analyses, individuals were treated as random effects to allow individual variation in intercept. But since individual reaction norm slopes vary due to variation in individual phenotypic plasticity, we tested for individual variation in reaction norm slopes by fitting additional MCMCglmms with different random effect structures (Nussey et al. 2007). Model 1 allowed individual variation in intercept (between-individual variance in intercepts = $V_{\mathrm{ind0}} \neq 0$) and common slopes across all individuals (between-individual variance in slopes = $\mathrm{Var}_{\mathrm{ind1}} = 0$). Model 2 allowed individual variation in intercept and slope ($\mathrm{Vi}_{\mathrm{nd0}} \neq 0$, $\mathrm{Var}_{\mathrm{ind1}} \neq 0$). Individuals exhibit variation in phenotypic plasticity when model 2 receives better support (lower DIC) than model 1. If model 1 received the lowest DIC, this would suggest high between-individual variation in behavior, but low variation in individual phenotypic plasticity. We report results of model comparisons (DICs are given in Table 3) together with the best fit, the model results for V_{ind0} and $\mathrm{Var}_{\mathrm{e}}$ (= residual variance) as well as $\mathrm{Var}_{\mathrm{ind1}}$, when applicable.

Composition of aggressiveness types in high densities and survival

We have previously shown in *L. sclopetarius* that groups varying in the composition of individual aggressiveness type differ in number of survivors under high density conditions (Kralj-Fišer and Schneider 2012). Here we conducted similar experiments in *Z. x-notata* and *N. umbratica*. According to the aggressiveness scores, we composed three classes of groups: (i) aggressive groups, (ii) non-aggressive groups, and (iii) mixed groups. Each group consisted of seven adult individuals (five females and two males), as this density has been previously shown to result in cannibalistic events and/or starving (Kralj-Fišer and Schneider 2012), thus creating a challenging environment for these spiders. Aggressive groups were composed of spiders from the upper third of the aggression score distribution (no. of groups: *Z. x-notata* = 6; *N. umbratica* = 6). Non-aggressive groups were composed of spiders from the lower third of the aggression score distribution (no. of groups: *Z. x-notata* = 5; *N. umbratica* = 6). Finally, the mixed group was composed of randomly selected spiders that had not gone through aggressiveness scoring (no. of groups: *Z. x-notata* = 5; *N. umbratica* = 7). All individuals were weighed a day prior to the experiment to assure similar body sizes of individuals in the same group. Groups were housed in terraria (36 × 36 × 6 cm) and were provided with identical prey regimes (14 flies) twice a week. We checked for cannibalized spiders three times per week, and removed remains of dead individuals. After 21 days, mortality and individual body weight of surviving spiders were assessed.

Statistical analyses

We tested for the effect of treatment (different group compositions: aggressive, non-aggressive, mixed) on the estimated individual weight changes, $\left(\frac{final\ average\ individual\ mass - start\ average\ individual\ mass}{start\ average\ individual\ mass}\right)$, and the number of survived spiders using Kruskal-Wallis tests. The average individual weight was used since we could not identify individual spiders after 21 days. We used the Mann-Whitney *U* test when comparing two groups.

Results

Between and within-species behavioral variation

Between-species behavioral variation

1. Activity in a novel environment

The three species differed in the duration of initial activity in a novel environment (species: Wald $\chi^2 = 37.142$, df = 2, $P < 0.001$; sex: Wald $\chi^2 = 0.087$, df = 1, $P = 0.768$; species*sex: Wald $\chi^2 = 4.928$, df = 2, $P = 0.085$; $N = 217$; Table 1; Fig. 1). As predicted, *L. sclopetarius* were active for the longest period in the novel environment and *Nuctenea umbratica* exhibited the shortest activity (Table 1). The duration of activity in *L. sclopetarius* was not significantly higher than in *Z. x-notata* (Table 1; Fig. 1).

We found no between-sex differences in duration of initial activity in a novel environment in any of the three species; however, individuals differed significantly in duration of initial activity when placed in a novel environment for the first vs. second time (Table 2). While *L. sclopetarius* spiders increased activity durations, *Z. x-notata* and *N. umbratica* exhibited shorter activity in their second trial (Table 2).

2. Aggressiveness towards same-sex conspecific

The aggression scores differed among species, sexes, and their interaction (species: Wald $\chi^2 = 46.494$, df = 2, $P < 0.001$; sex: Wald $\chi^2 = 93.949$, df = 1, $P < 0.001$; species*sex: Wald $\chi^2 = 1.208$, df = 2, $P = 0.547$; $N = 207$). Across all species, males were more aggressive than females (mean difference = 14.18, SE = 1.799, $P < 0.001$). The most aggressive species were *Z. x-notata*, followed by *L. sclopetarius*, and the least aggressive were *N. umbratica* (Table 1; Fig. 1). The aggressiveness levels did not differ between the two repeated trials (Table 2).

Within-species behavioral variation

1. Activity in a novel environment

We found significant between-individual variances in initial activity in *L. sclopetarius* (range = 1.8–298.23), *Z. x-notata* (range = 0–298.5), and *N. umbratica* (range = 0–95.44), i.e., DICs of constrained (without random factor) models were higher from DICs of unconstrained models (id as random factor) (Table 2). The individual differences in initial activity in a novel environment were significantly repeatable in *L. sclopetarius* (mean $r = 0.493$); *Z. x-notata* (mean $r = 0.426$), and *N. umbratica* (mean $r = 0.481$) (Table 2; Fig. 2).

2. Aggressiveness towards same-sex conspecific

The between-individual variation in aggressiveness was significant in all three species (*L. sclopetarius*, range = 0–76; *Z. x-notata*, range = 0–95; and *N. umbratica*, range = 0–94 Table 2). The individual differences in intra-sex aggressiveness appeared significantly repeatable, with the mean repeatability estimates 0.832, 0.838, and 0.781 in *L. sclopetarius*, *Z. x-notata*, and *N. umbratica*, respectively (Table 2; Fig. 2).

Table 1 Post hoc results of generalized estimating equation (GEE) testing for species differences in intra-sex aggressiveness ($N = 207$ individuals) and duration of initial activity when placed in a novel environment ($N = 217$ individuals)

Species (1)	Species (2)	Mean difference	Std. error	df	*P*	Lower 95% Wald CI for diff.	Upper 95% Wald CI for diff.
Initial activity in a novel environment							
L. sclopetarius	*Z. x-notata*	16.32	9.599	1	0.089	−2.48	35.15
L. sclopetarius	*N. umbratica*	34.88	6.143	1	**<0.001**	22.84	46.92
Z. x-notata	*N. umbratica*	18.55	7.620	1	**0.015**	3.62	33.48
Aggressiveness							
L. sclopetarius	*Z. x-notata*	−7.17	2.261	1	**0.002**	−11.61	−2.74
L. sclopetarius	*N. umbratica*	4.98	1.343	1	**<0.001**	2.34	7.61
Z. x-notata	*N. umbratica*	12.15	2.078	1	**<0.001**	8.08	16.22

Significant results (after correction for multiple comparisons) are bolded. Similar results were given by MCMCglmm (see Supplement 1)

Variation in individual phenotypic plasticity

Model 2, which included individual variation in intercept and slope, received better support than model 1, which included individual variation in intercept only (*L. sclopetarius*, m2: $V_{ind0} = 0.168$, $Var_{ind1} = 0.110$; $Var_e = 0.048$; *Z. x-notata*, m2: $V_{ind0} = 0.149$, $Var_{ind1} = 0.093$; $Var_e = 0.027$; *N. umbratica*, m2: $V_{ind0} = 0.142$, $Var_{ind1} = 0.08$; $Var_e = 0.051$; Table 3; Fig. 3). Namely, *L. sclopetarius*, *Z. x-notata*, and *N. umbratica* exhibited individual variation in phenotypic plasticity in initial activity in a novel environment. In other words, individuals differed in the degree of change in their activity levels when comparing their first exposure vs. the second exposure to novel environment test. Comparably, the results suggest that individuals exhibited high between-individual variation but low variation in plasticity in aggressiveness (*L. sclopetarius*, m1: $V_{ind0} = 1.53$, $Var_e = 0.21$; m2: $V_{ind0} = 0.11$, $Var_{ind1} = 0.34$; $Var_e = 0.12$; *Z. x-notata*, m1: $Var_{ind0} = 2.36$, $Var_e = 0.22$; m2: $V_{ind0} = 1.88$, $Var_{ind1} = 0.34$; $Var_e = 0.22$; *N. umbratica*, m1: $Var_{ind0} = 1.82$, $Var_e = 0.31$; m2: $V_{ind0} = 1.21$, $Var_{ind1} = 0.48$; $Var_e = 0.14$).

Behavioral correlations

The unconstrained and the constrained models had very similar DIC estimations. This implies that the between-individual and phenotypic correlations among aggressiveness and initial activity in a novel environment were non-significant (results are given in Table 4) in all tested species. See also Supplement 3.

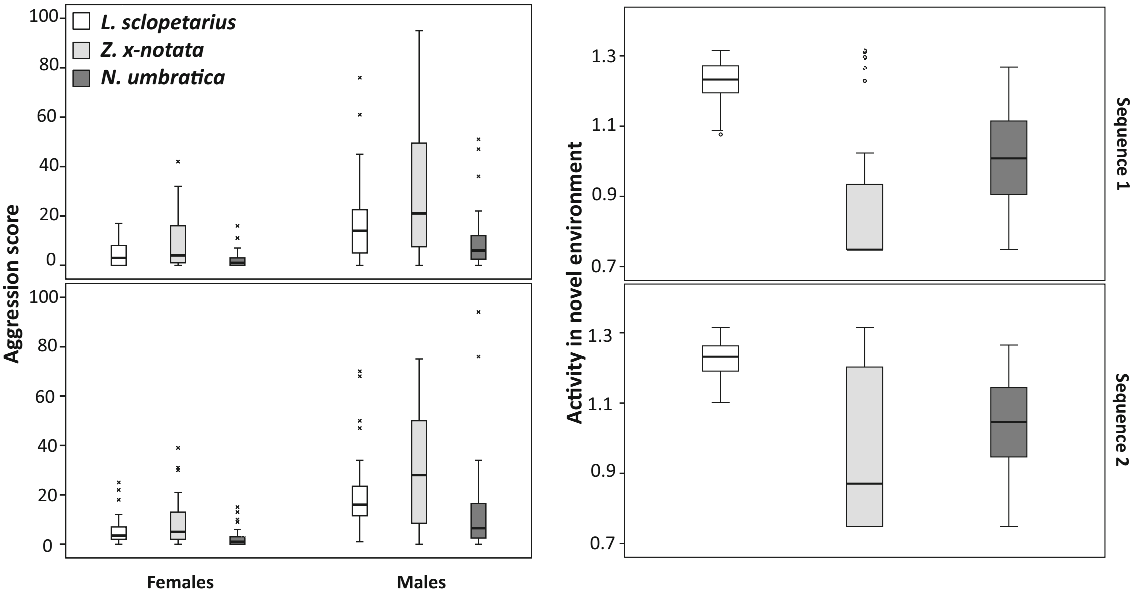

Fig. 1 Intra-sex aggressiveness scores and durations of initial activity in a novel environment (Box-Cox transformed) in the three tested species. The *above panels* represent data from the first test (sequence 1), the *below panels* show data from the repeated test (sequence 2). Species differences are given in Table 1

Table 2 Results of MCMCglmm estimating variance components of measured behaviors (aggressiveness, latencies to stop activity when placed into the novel environment) with fixed (sequence, sex) and random effects (id)

		Post. mean	l-95% CI	u-95% CI	pMCMC
Aggressiveness					
L. sclopetarius	(Intercept)	−0.732	−1.450	0.282	0.14
	Sequence	0.202	−0.006	0.427	0.12
	Sex	**1.507**	**0.920**	**1.906**	**<0.01**
	Between-individual variance	**0.996**	**0.553**	**1.620**	
	Within-individual variance	0.237	0.119	0.345	
	Repeatability	**0.832**	**0.679**	**0.930**	
Z. x-notata	(Intercept)	0.356	−0.666	1.553	0.62
	Sequence	0.076	−0.145	0.272	0.46
	Sex	**1.091**	**0.339**	**1.901**	**<0.01**
	Between-individual variance	**2.172**	**1.320**	**3.307**	
	Within-individual variance	0.340	0.156	0.547	
	Repeatability	**0.838**	**0.763**	**0.942**	
N. umbratica	(Intercept)	−1.817	−2.732	−0.745	<0.01
	Sequence	0.207	−0.025	0.427	0.14
	Sex	**1.660**	**1.103**	**2.178**	**<0.01**
	Between-individual variance	**1.209**	**0.800**	**1.939**	
	Within-individual variance	0.332	0.182	0.551	
	Repeatability	**0.781**	**0.632**	**0.890**	
Initial activity in a novel environment					
L. sclopetarius	(Intercept)	2.057	1.795	2.314	<0.01
	Sequence	**0.118**	**0.040**	**0.195**	**<0.01**
	Sex	0.168	−0.011	0.322	0.08
	Between-individual variance	**0.082**	**0.034**	**0.134**	
	Within-individual variance	0.068	0.052	0.099	
	Repeatability	**0.493**	**0.339**	**0.692**	
Z. x-notata	(Intercept)	1.122	0.932	1.402	<0.01
	Sequence	**−0.141**	**−0.230**	**−0.062**	**<0.01**
	Sex	−0.096	−0.221	0.037	0.12
	Between-individual variance	**0.024**	**0.007**	**0.055**	
	Within-individual variance	0.049	0.037	0.085	
	Repeatability	**0.426**	**0.107**	**0.592**	
N. umbratica	(Intercept)	0.682	0.493	0.857	<0.01
	Sequence	−0.046	−0.107	0.002	0.10
	Sex	0.058	−0.068	0.138	0.28
	Between-individual variance	**0.455**	**0.027**	**0.068**	
	Within-individual variance	0.052	0.036	0.061	
	Repeatability	**0.481**	**0.336**	**0.632**	

The significant effects of the fixed factors ($P < 0.05$) are bolded. To estimate the significance of between-individual variance in intercept or elevation, we compared constrained (without random factor) and unconstrained models (id as random factor), and defined significance when DIC (deviance information criterion) unconstrained − DIC constrained <5. We calculated adjusted repeatability and their 95% credible intervals (CI). Significant estimates are bolded. Detailed results are given in Supplement 1

Composition of aggressiveness types in high densities and survival

We aimed to further test the importance of between-individual variation in aggression for survival in high density conditions. Higher numbers of *N. umbratica* vs. *Z. x-notata* spiders survived under high density conditions for 3 weeks ($F_{34,1} = 34.817$, $P < 0.001$; Fig. 4). The average individual mass at the end was higher than the average individual mass at the start of high density experiment in *N. umbratica* (Wilcoxon $Z = -3.823$, $P < 0.001$, $N = 19$), but not in *Z. x-notata* (Wilcoxon $Z = -0.621$, $P = 0.535$, $N = 15$; Fig. 4).

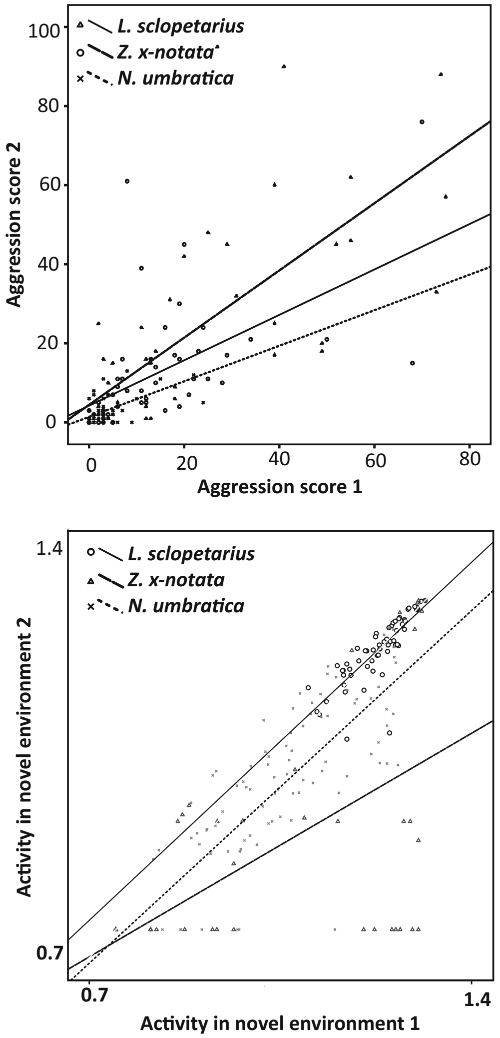

Fig. 2 Aggressiveness scores (*above*) and durations of initial activity in a novel environment test (Box-Cox transformed) (*below*), in the first and second repeats in *L. sclopetarius*, *Z. x-notata*, and *N. umbratica*. Results are given in Table 2

While we found no differences in survivorship between group classes in *N. umbratica* when exposed to high density conditions for 3 weeks (Kruskal-Wallis test, $\chi^2 = 1.303$, df = 2, $P = 0.521$), the group classes in *Z. x-notata* significantly differed in number of survived individuals (Kruskal-Wallis test, $\chi^2 = 9.551$, df = 2, $P = 0.008$; Fig. 4). In *Z. x-notata*, the groups of mixed individuals had significantly higher survivorship than groups consisting of only aggressive (Mann-Whitney $U = 1$, $N = 11$, $p = 0.009$) or only non-aggressive individuals (Mann-Whitney $U = 0$, $N = 10$, $p = 0.007$); however, there was no difference between aggressive and non-aggressive groups (Mann-Whitney $U = 11$, $N = 10$, $P = 0.841$; Fig. 4).

While the change in average individual mass did not differ among groups in *N. umbratica* (Kruskal-Wallis test, $\chi^2 = 0.853$, df = 2, $N = 19$, $P = 0.653$), we found significant differences between groups in *Z. x-notata* (Kruskal-Wallis test, $\chi^2 = 6.146$, df = 2, $P = 0.046$); namely, survivors in the groups of aggressive individuals had decreased mass, in groups of non-aggressive individuals survivors exhibited increased mass, and in the mixed groups survivors did not change the mass. The change in average individual mass differed significantly between aggressive and non-aggressive groups (Mann-Whitney $U = 3$, $N = 11$, $P = 0.03$), but did not differ between non-aggressive and mixed groups (Mann-Whitney $U = 4$, $N = 10$, $P = 0.095$), or between aggressive and mixed groups (Mann-Whitney $U = 9$, $N = 11$, $P = 0.329$).

Discussion

In this study, we contrast behavioral variation among three orb-web spider species that commonly occur along an urban to suburban gradient: *Larinioides sclopetarius*, an urban exploiter, dominant in its habitat; *Zygiella x-notata* that mainly dwells in human-altered areas; and *Nuctenea umbratica* that lives on trees in urban and suburban environments. We compared *L. sclopetarius* from urban areas to suburban *Z. x-notata* and *N. umbratica*, and found these species to differ in their average levels of activity in a novel environment and

Table 3 Deviance information criteria of candidate models

	L. sclopetarius	*Z. x-notata*	*N. umbratica*
Aggressiveness			
Model 1: random = ~ID	**654.65**	**682.24**	**726.30**
Model 2: random = ~idh(1 + sequence):ID	655.87	682.54	726.92
Initial activity in novel environment			
Model 1: random = ~ID	71.55	21.82	105.76
Model 2: random = ~idh(1 + sequence):ID	**51.21**	**9.10**	**94.21**

All models were fit with sequence number as a fixed effect, and differ in their random structure. Model 2 includes common slopes but allows individual variation in intercepts; model 2 allows individual variation in intercept and slope. The models with the lowest DIC are bolded. Individuals exhibit individual variation in behavioral plasticity when model 2 receives better support. In case that model 1 receives the lowest DIC, data suggest high between-individual variation in behavior, but low individual variation in behavioral plasticity

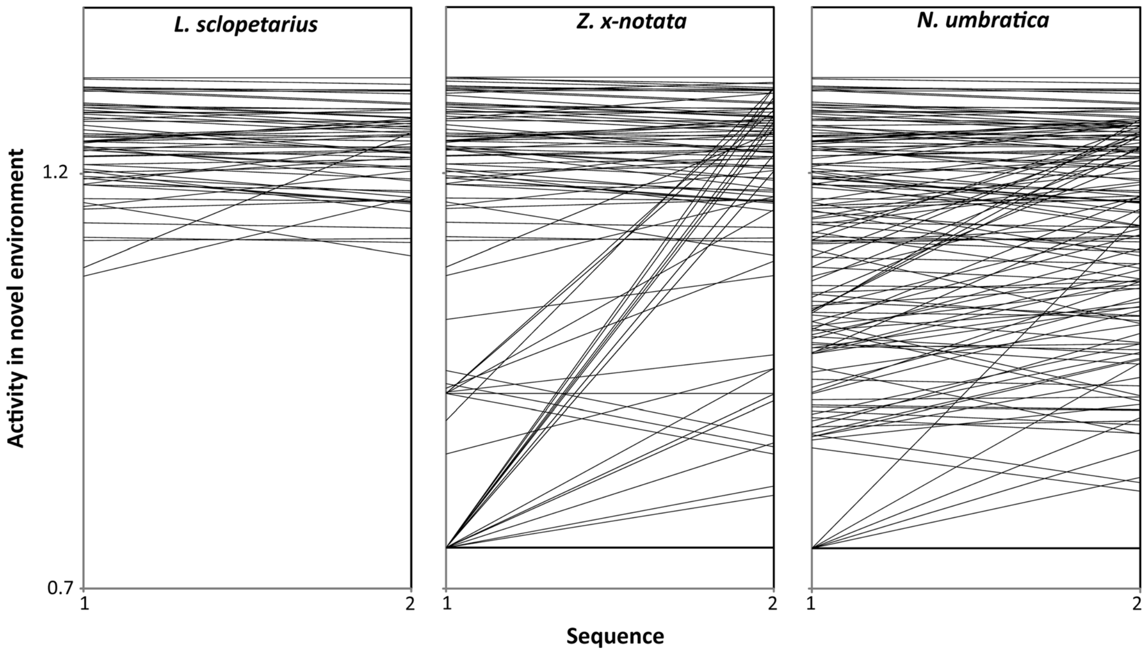

Fig. 3 Durations of initial activity (Box-Cox transformed; *y-axis*) in the first and repeated novel environment test (*x-axis*: 1 and 2) in *L. sclopetarius*, *Z. x-notata*, and *N. umbratica*. *Lines* represent individuals' reaction norm slopes

aggressiveness, but to exhibit similarities in relation to within- and between-individual variation in behavior.

Comparing species average behavior levels, we detected that *L. sclopetarius* exhibited the highest activity in the novel environment and *N. umbratica* the lowest, while *Z. x-notata* exhibited intermediate activity. Scientists often equate an animal's reaction to novelty, such as a novel environment, to its boldness, e.g., in response to predator exposure (Huntingford 1976; Bell and Stamps 2004; Kortet and Hedrick 2007). Boldness, in turn, is hypothesized to enable an organism to adapt to urban environments (reviewed in Miranda et al. 2013). Indeed, research on other organisms has found that individuals in urban populations exhibit reduced fear of novel stimuli as compared to those in rural populations (e.g., *Passer domesticus*, Martin and Fitzgerald 2005; *Acridotheres tristis*, Sol et al. 2011; reviewed in Miranda et al. 2013), supporting the idea that boldness might enable adaptation to urban

Table 4 Results of bivariate MCMCglmm testing for between-individual and phenotypic correlations of aggressiveness and initial activity in a novel environment in the three species

Species	Between-individual correlation	Phenotypic correlation
L. sclopetarius	0.190	0.112
Z. x-notata	−0.080	0.024
N. umbratica	0.285	0.145

We compared constrained models (co-variances between and within individuals are constrained to zero; $Cov_{ind_{0y},ind_{0z}} = 0$, $Cov_{e_{0y},e_{0z}} = 0$) and unconstrained models ($Cov_{e_{0y},e_{0z}} = 0$) and assumed significant correlation when DIC unconstrained − DIC constrained <5. All correlations were insignificant. DIC of unconstrained model was slightly smaller (*L. sclopetarius*: ΔDIC = 0.64; *N. umbratica:* ΔDIC = 1.19). Detailed results are given in Supplement 3

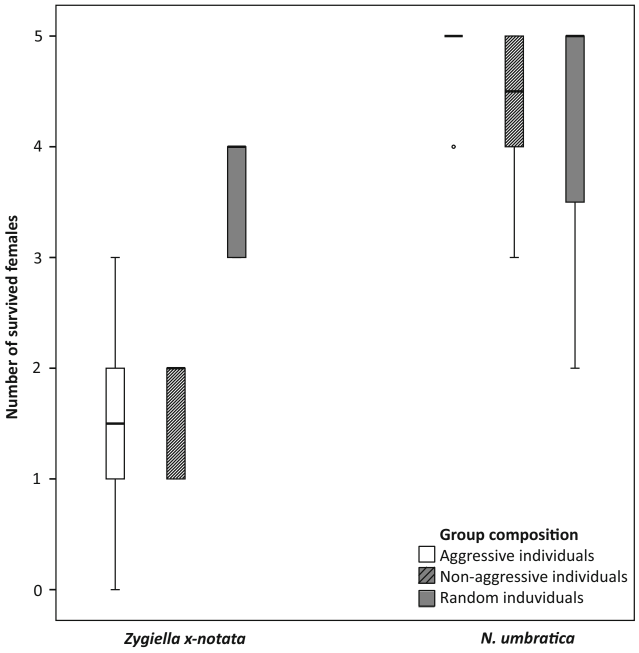

Fig. 4 Boxplots represent data from the three different group compositions (only aggressive individuals, only tolerant individuals, random individuals) exposed to high density conditions for 21 days for *Z. x-notata* and *N. umbratica*. Differences between group compositions in the number of survived females: *Z. x-notata* (Kruskal-Wallis test, χ^2 = 9.551, df = 2, *N* = 16, *P* = 0.008) and *N. umbratica* (Kruskal-Wallis test, χ^2 = 1.303, df = 2, *N* = 19, *P* = 0.521)

environments. Our results are consistent with this idea, as *L. sclopetarius*, our focal urban species, was also the most active in our novel environment. Such increased activity in a novel environment, or potential boldness, may also bring associated costs, i.e., when animals are overly active in the presence of a predator or other threats (Wilson 1998; Sih et al. 2003). For *L. sclopetarius*, however, boldness may bear little cost related to predator exposure. Natural predators and responses to predation risk have not been assessed in these species or populations, but it has been suggested previously that *L. sclopetarius* have few natural predators (Kleinteich 2010). Regardless, additional studies are required to test the potential costs associated with increased activity in *L. sclopetarius.*

Contrary to our expectations, *Z. x-notata* exhibited the highest levels of within-species aggressiveness followed by *L. sclopetarius* and then *N. umbratica.* Our initial expectation was that the most urban species, and that with the highest population densities (*L. sclopetarius*), would be the most tolerant, or exhibit the lowest levels of aggression. While aggressiveness may generally be beneficial in territorial disputes, overt aggressiveness may be costly in high density populations due to high incidences of injury and low survival rate (Holway 1998; Kralj-Fišer and Schneider 2012). This potential cost of aggressiveness may help explain observed differences in population density between *L. sclopetarius* and *Z. x-notata*. *Zygiella x-notata* can indeed be found in large aggregations in the field (Leborgne and Pasquet 1987), but they always exhibit a lower density of individuals as compared to aggregations of *L. sclopetarius* (Leborgne and Pasquet 1987; Schmitt and Nioduschewski 2007a, 2007b). A higher level of aggressiveness in *Z. x-notata* may help explain these differences in density. Following this line of reasoning, we would expect *N. umbratica*, the most solitary species, to exhibit high levels of aggression. In contrast, we found *N. umbratica* to be inherently non-aggressive and to avoid conspecifics. Based upon these results, we propose that their observed isolation in nature is due, at least in part, to their web structure and not their level of aggression. *Nuctenea* spiders build relatively large orb webs that catch sizeable prey (Bucher and Entling 2011), and such webs likely require more structured habitat. Previous studies support this idea, as increased densities of *N. umbratica* individuals, in combination with lack of space, led to individuals in poor body condition (Bucher and Entling 2011). Ultimately, while aggressiveness level did not exactly conform to our predictions of urban invasion, our data do suggest that level of within-species aggressiveness might play a role in determining population density once an environment is colonized for some species while others might be constrained by habitat structure.

Beyond average behavior levels across species, previous studies have emphasized the importance of between-individual variation in behavior for successful exploitation of urban environments (Møller 2010; Carrete and Tella 2011; Bókony et al. 2012). For example, Møller (2008) found that bird species that initially colonized urban areas had more variable behavior than those that failed in such colonization. Along similar lines, Fogarty et al. (2011) suggested that different behavioral types are favored during invasion process, e.g., bold and aggressive individuals are good initial dispersers, whereas shy and socially tolerant individuals may cause subsequent population proliferation (e.g., Clobert et al. 2009; Cote et al. 2010). In at least partial agreement with these studies, we observed species-level differences in activity level (highest in the urban species *L. sclopetarius*) simultaneous with significant between-individual variation in activity and within-sex aggressiveness in all three tested species. We propose that the higher activity level of *L. sclopetarius* might have enabled their initial colonization of urban areas, as compared to the other two species. Subsequently, as new individuals immigrated and the population grew, variation among individuals in activity and aggression may have facilitated increases in population density in *L. sclopetarius*. The individual differences were stable over time with the repeatability estimates ranging from 0.43 to 0.49 for activity in a novel environment, and from 0.78 to 0.83 for aggressiveness, which is concordant with results from comparable invertebrate and vertebrate studies (Kralj-Fišer et al. 2007, 2012; Pruitt et al. 2008; Bell et al. 2009).

In comparison to repeatability estimates for aggressiveness, spiders of all three species exhibited considerably lower (but still significant) repeatability in activity when introduced to a novel environment. This comparably lower repeatability estimate is mainly due to higher within-individual variation, namely, higher average plasticity. The pattern of change in activity to a novel environment across two exposures also differed across species. While *L. sclopetarius* prolonged the activity in the second trial, *Z. x-notata* and *N. umbratica* shortened their activity durations. It is possible that *L. sclopetarius* were desensitized/habituated due to repeated trials, whereas *Z. x-notata* and *N. umbratica* responses might reflect sensitization. Alternatively, the species may differ in their risk assessment of the new environment—e.g., given that no predator were encountered, *L. sclopetarius* may have estimated the environment to be safe, while *Z. x-notata* and *N. umbratica* may require additional information before attaining the same risk estimate. Other explanations exist, but it seems likely that regardless of the underlying reason for the behavioral change, the altered responses likely result from learning (Barron et al. 2015). Within species, we observed additional variation as individual spiders did not respond uniformly but differed in degrees of behavioral change across the two repeated trials. In contrast to our prediction that estimates of between-individual variance in reaction norm slopes should be higher in the strictly urban *L. sclopetarius* compared to *Z. x-notata* and *N. umbratica*, we found that the three species exhibited comparable levels of individual variation in behavioral plasticity. One potential interpretation of these results is that (variation in) behavioral change in reaction to novel vs. familiar stimuli may be adaptive in both city exploiters as well as in suburban species.

The estimates of between-individual variance were remarkably high for aggressiveness in all three species, implying that different aggressiveness types are present in urban and suburban species, regardless of whether they occur in high density aggregations or not. Our results from "high density experiments" support the hypothesis that consistent between-individual variation in aggressiveness enhances survival in high density groups. As in *L. sclopetarius* (Kralj-Fišer and Schneider 2012), groups of *Z. x-notata* consisting of both aggressive and tolerant spiders had higher survival rates over 3 weeks than the groups composed of either aggressive or tolerant individuals. However, in *N. umbratica*—the species for which individuals typically occur in isolation—survival rates were very high and did not differ among groups of different aggressiveness type compositions. Additionally, in contrast to an earlier study that documented a decrease in body condition with increased density in *N. umbratica* (Bucher and Entling 2011), we observed increased body mass after 3 weeks. Perhaps, a longer exposure to high density conditions would give more informative results.

The results for *A. x-notata* are consistent with the suggestion that urban environments favor populations that consist of individuals exhibiting diverse, but stable, aggressiveness types, which may facilitate high density aggregations. Variation in behavioral types within the groups, in particular in social animals, has been repeatedly shown to enhance group fitness, e.g., through better survival and/or increased reproductive success (Watters and Sih 2005; Jones et al. 2010; Pruitt and Riechert 2011), increased group productivity (Modlmeier and Foitzik 2011; Modlmeier et al. 2012), or task proficiency (Wright et al. 2014; Laskowski et al. 2016). Various mechanisms have been proposed to explain why diverse groups outperform monotypic groups (Wolf and Weissing 2012; Montiglio et al. 2013). In orb-web spiders, individuals of different aggressiveness types may vary in their distribution within habitats resulting in non-random interactions among behavioral types, reduced competition among individuals, and consequently more diverse habitat use (e.g. Kobler et al. 2009). In our experiments in *Z. x-notata*, for example, in the "aggressive groups," most individuals might compete for the prime sites (frame corners), whereas in the mixed groups, tolerant individuals might leave these sites to the aggressive ones and settle elsewhere. While the aggressive groups suffered high mortality rates due to intense antagonistic interactions, aggressive individuals were far enough from each other to reduce competition in the mixed group. In the "tolerant group," survival rates resembled those in "aggressive groups," yet individuals gained body mass in the former and decreased it in the latter. This suggests that, at least in the laboratory conditions, groups of tolerant individuals do better than groups of aggressive individuals. Additional field experiments are needed to investigate the mechanisms allowing mixed aggressive type groups to outperform groups of tolerant or aggressive individuals only, perhaps related to functional complementary or niche partitioning.

Finally, we failed to find significant correlations between activity in a novel environment and aggressiveness, implying that the two behavioral traits can vary independently in all three species. Several studies comparing rural and urban populations have found behavioral correlations in rural, but not in urban, conspecific populations (Evans et al. 2010; Scales et al. 2011; Miranda et al. 2013); however, we found no behavioral associations in either urban or suburban spiders. This suggests that the association between behavioral traits is more flexible in (sub)urban than rural environments. In other words, urbanization may lead to breakdown of behavioral syndromes, which probably occurs through behavioral plasticity (Bell and Sih 2007; Dingemanse et al. 2007; Bengston et al. 2014; Royauté et al. 2015).

Conclusions

Prior and current evidence suggests that the ultimate city exploiter among orb-web spiders, *L. sclopetarius*, is a bold, active, and moderately aggressive species with high developmental plasticity, a short life cycle, and high reproductive output (Mayntz et al. 2003; Kleinteich and Schneider 2011; Kralj-Fišer et al. 2014). In comparison, the synanthropic species, *Z. x-notata*, exhibits high aggressiveness, but lower levels of boldness and less plastic development (Mayntz et al. 2003). Finally, the suburban *N. umbratica* is non-aggressive and relatively inactive in novel environments, with a rather canalized development and longer life cycle (Kralj-Fišer et al. 2014). Despite these differences, the three species exhibit similar levels of variation in behavioral traits both between and within individuals. In the urban and suburban species, the between-individual differences in aggressiveness appeared highly repeatable, indicating that variation in aggressiveness types likely enables survival in high density conditions. We found the evidence for both consistent individual differences and plasticity in individuals' response to a novel environment, suggesting that some degree of flexibility in reaction to novelty may be crucial when adapting to urbanized environment. We conclude that urban populations exhibit a complex pattern of behavioral flexibility and behavioral stability, and that their relative roles may depend on the function of any given behavior.

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All data analyzed during this study are included in this published article and its supplementary information file 4.

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