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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.

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 & MacIsaac 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 m^2 (Nioduschewski & Kraayvanger 2005). Hence, high intraspecies 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