

Development and growth in synanthropic species: plasticity and constraints

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Abstract Urbanization poses serious extinction risks, yet some species thrive in urban environments. This may be due to a pronounced developmental plasticity in these taxa, since phenotypically, plastic organisms may better adjust to unpredictable urban food resources. We studied phenotypic plasticity in *Nuctenea umbratica*, a common European forest and urban vegetation spider. We subjected spiderlings to low (LF), medium (MF) and high (HF) food treatments and documented their growth and developmental trajectories into adulthood. Spiders from the three treatments had comparable numbers of instars and growth ratios, but differed in developmental periods. Longest developing LF spiders (♀=390, ♂=320 days)

had the smallest adults, but MF (♀=300, ♂=240 days) and HF (♀=240, ♂=210 days) spiders reached comparable adult sizes through shorter development. While males and females had comparable instar numbers, females had longer development, higher growth ratios, adult sizes and mass; and while males adjusted their moulting to food availability, female moulting depended on specific mass, not food treatment. We discussed the patterns of *Nuctenea* sex-specific development and compared our results with published data on two other Holarctic urban colonizers (*Larinioides sclopetarius*, *Zygiella x-notata*) exhibiting high plasticity and fast generation turnover. We conclude that despite relatively unconstrained developmental time in the laboratory enabling *Nuctenea* to achieve maximal mass and size—main female fitness proxies—their relatively fixed growth ratio and long generation turn-over may explain their lower success in urban environments.

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Introduction

Among human-induced environmental changes, urbanization currently represents one of the major threats to Earth's biodiversity. Urbanization causes loss or fragmentation of native habitats, modifications in community structures, pollution, and changes in sensory environments (McKinney 2002, 2008). In urban environments, food resources become spatially concentrated and their temporal availability oscillates more arbitrarily (Shochat et al. 2006; Sol et al. 2013). While human-induced changes imperil most taxa and place their populations at risk of extinction, some organisms thrive in urban environments, proliferating and expanding their ranges (McKinney 2002, 2008). This raises the question of what mechanisms enable them to tolerate urban environmental alterations.

Phenotypic plasticity, the ability of an organism to change a phenotype in response to variation in the environment (West-Eberhard 2003), may be a salient quality of those species that thrive in cities (Sol 2003; Yeh and Price 2004). The important components of phenotypic plasticity are adjustable life history traits, such as developmental and growth patterns, size and age at maturation, reproductive investment, and longevity (Stearns 1992; Roff 2002). Organisms that are able to adjust life histories to rapid environmental changes are expected to fare better in urban environments than individuals with more canalized life history trajectories (e.g. Buczkowski 2010; Kleinteich and Schneider 2011). In the latter, developmental traits show low ability for phenotypic changes in response to environmental conditions. However, both plasticity and canalization have fitness costs and benefits (Van Buskirk and Steiner 2009; Dmitriew 2011).

Developmental and growth patterns determine age and size at maturity, which significantly affect fitness (Stearns 1992; Roff 2002). For instance, the growth rate and developmental times affect vulnerability to predators' exposure (Gotthard 2000) and determine a population's generation time. In most arthropods, female adult mass—strongly correlated with fecundity (Suter 1990; Higgins 1992; Head 1995)—affects the net reproductive rate, R (mean number of female offspring a mother produces during her lifetime) whereas in males, size at maturity strongly relates to competitive abilities in male–male contests and female choice (Christenson and Goist 1979; Vollrath 1980; Andersson 1994). Finally, the net reproductive rate and generation time strongly relate to intrinsic rate of population, r (i.e. per capita rate of population increase).

In arthropods, the exoskeleton grows in discrete steps through moulting, whereas mass changes continuously (Foelix 2010). According to Dyar's rule (Dyar 1890), arthropods exhibit a determined (also “canalized”) growth rate quantified as the ratio of two consecutive instar sizes (Przibram and Megušar 1912; Cole 1980) and are often considered to have a constant number of instars (Esperk et al. 2007). Growth plasticity, on the other hand, refers to variation in growth rates in response to variation in environmental conditions. A number of studies in arthropods have investigated the effects of environmental conditions on variation in developmental trajectories and growth rate (e.g. Gimnig et al. 2002; Gilles et al. 2010; Kleinteich and Schneider 2011), in particular, in response to different temperature regimes (e.g. Li and Jackson 1996; Robinson and Partridge 2001; Flenner et al. 2010). In insects, studies of growth and developmental plasticity depending on diet regimes have yielded mixed results. While in some taxa exhibiting fixed instar numbers Dyar's rule receives support (e.g. *Acrida exaltata*, Ahmad 2012; *Dendroctonus valens*, Liu et al. 2014), other taxa show significant plasticity in growth rates and developmental trajectories depending on food supply (Atkinson and Sibly 1997; Esperk et al. 2007).

Detailed studies revealed considerable species differences in degrees of plasticity among developmental parameters, and various parameters are often interdependent (e.g. Davidowitz and Nijhout 2004). Higgins and Rankin (1996) described eight possible combinations of canalized and plastic developmental and growth parameters in arthropods resulting in various outcomes regarding age and size at maturity. Four of these combinations (canalized inter-moult duration, canalized instar number, canalized growth rate and fully plastic developmental pattern) were documented in empirical field research (Higgins and Rankin 1996). For instance, the hawkmoth, *Manduca sexta*, exhibits canalized maximum inter-moult duration, but plasticity in instar number, growth rate and pre-moult mass in response to diet (Nijhout and Willams 1974; Nijhout 1975; Safranek and Williams 1984). The well-fed individuals might develop at higher growth rates and might be able to reach critical mass for pupation and metamorphosis through fewer instars (Kingsolver 2007). On the other hand, poor nutrition in *M. sexta* might lead to moulting after certain critical number of days even in the absence of mass gain. In the milkweed bug, *Oncopeltus fasciatus*, the number of instars is fixed, but the inter-moult duration and growth rates are plastic (Nijhout 1979), and thus, well-fed individuals develop earlier and at a higher mass.

Substantial difference in male and female body size is often attributed to sex-specific selection, e.g. scramble competition and male–male competition in males, and fecundity selection in females (Andersson 1994; Head 1995; Blanckenhorn 2005; Blanckenhorn et al. 2007). At proximate level, size dimorphic species exhibit sex-specific differences in growth and development and also sex variation in plasticity in response to environmental variation (reviewed in Stillwell et al. 2010). For example, in *M. sexta*, males and females differ in plasticity in the parameters critical for adult body size, i.e. growth rate and critical mass for metamorphosis, in response to diet and temperature (Stillwell and Davidowitz 2010).

Little is known about growth and developmental plasticity in spiders, a species rich and ecologically important invertebrate clade-important terrestrial predators of insects and known for some spectacular cases of female-biased sexual size dimorphism (e.g. Kuntner et al. 2012). In spiders, growth and development are believed to largely depend on food availability (Miyashita 1968). Cursorial spiders actively search for food sources and seem to mostly exhibit plastic growth and development patterns (e.g. Miyashita 1968; Enders 1976; Li and Jackson 1997). On the other hand, orb-web spiders are sit-and-wait predators whose ability to behaviourally adjust to prey availability is limited to changing web site, web position, and web properties (Herberstein and Elgar 1994; Heiling and Herberstein 1998; Blackledge et al. 2011). While this may suggest that they should be even more adapted to temporal variations in foraging opportunities, the results from empirical studies show ranges of growth and

developmental plasticity in orb weavers. For example, the bridge spider (*Larinioides sclopetarius*) exhibits extreme plasticity depending on food availability and fluctuation in virtually all life history traits (Kleinteich and Schneider 2011), and comparable plasticity was reported in *Zygiella x-notata* (Mayntz et al. 2003), another synanthropic orb weaver. On the other hand, while the neotropical *Nephila clavipes* shows constant growth per ecdysis and pre-moult mass, its number of moults and inter-moult duration are plastic (Higgins 1992, 1993; Higgins and Rankin 1996). Since only a handful of species have been investigated, it is premature to attribute synanthropic life styles to different degrees of phenotypic plasticity, although the conjecture is logical. Developmental and growth plasticity may have important ecological consequences and may significantly predict success of species in urban environments with buffered seasonality (and thus prolonged food availability), but often spatially and temporally unpredictable food resources (Shochat et al. 2006; Kearney et al. 2010).

To investigate these issues more closely, we asked if growth and developmental plasticity depending on food availability differ between three orb-web spiders that vary in their success as urban colonizers. We studied *Nuctenea umbratica* and compared our results with the published data on two other urban dwellers, *L. sclopetarius* (Kleinteich and Schneider 2011) and *Z. x-notata* (Mayntz et al. 2003). All three species are orb-weaving spiders whose females may be found year round in European urban areas but whose abundances vary. The synanthropic *L. sclopetarius* and *Z. x-notata* are successful colonizers of cities throughout the Holarctic, their preferred web sites are bridges, buildings, and other constructions. Their success in the urban environment has been hypothesised to be a consequence of their ability to adjust growth and development to temporal fluctuations of prey (Mayntz et al. 2003; Kleinteich and Schneider 2011). On the other hand, the study species, *Nuctenea umbratica* is a ubiquitous European forest dweller that also lives synanthropically, but in highly urbanized areas is either outcompeted by *L. sclopetarius* and *Z. x-notata*, or is confined to habitat patches with low population densities; in cities, they occupy trees and hedgerows in areas without artificial light (own data). We hypothesized that *Nuctenea* is poorly pre-adapted for urban habitats due to lower levels of growth and developmental plasticity (hence, more canalized) compared with *Larinioides* and *Zygiella*.

Materials and methods

Study object

The walnut orb weaver, *Nuctenea umbratica*, is a common Central European spider. These sizable spiders disperse by ballooning in juvenile stage and prefer landscapes with semi-

open habitats, such as forest edges, hedgerows, orchards and single trees (Bucher et al. 2010). While adult phenology peaks between June and October, females can be found year long (Nentwig et al. 2014). During the day, the spider hides under cracks in the bark of trees or fences with a signal line connected to its orb web, but assume a night foraging pose at web hub. We collected subadult spiders from their webs on trees and hedgerows along the Ljubljanica riverbank in Ljubljana, Slovenia, between May and July 2010.

Rearing conditions

Spiderlings used in laboratory assays originated from 41 females that had been raised to adulthood and had mated (one virgin male+one virgin female). We kept the egg sacs at room temperature and sprayed them with water three times a week. From 10 to 15 days after hatching, spiderlings were separated and placed into 250-ml plastic cups, then randomly subjected to three feeding regimes: low food (LF; $N=57$), medium food (MF; $N=45$) and high food (HF; $N=64$). The spiderlings in LF received one *Drosophila* fly once a week, those in MF one fly twice a week and those in HF two flies twice a week. After the fifth moult, we offered juvenile spiders the same number of prey as above, but substituted fruit flies for blowflies (*Calliphora* sp.) to secure their increased nutritional requirements. We checked each spider five times a week for moulting following their second moult (first moulting occurs in the egg sac about 3 days after hatching). Any spider that had moulted was weighed using an electronic balance to an accuracy of 0.001 g. From December 2011 to June 2013 we monitored the development of 166 individuals. Of these, 81 spiders reached adulthood ($N_{\text{♀}}=49$, $N_{\text{♂}}=32$; HF=33, MF=27, LF=21), 34 died and 51 were lost. At maturity, we fixed the spiders in 70 % ethanol and microscopically measured the length of their first patella+tibia and the carapace width.

Developmental and growth parameters

We documented the following parameters for each individual: *number of instars*, *developmental time* (time from hatching to adulthood), *mean inter-moult duration*, *mean growth ratio*, as well as *mass* and *size at maturity*. The proxy for size at maturity was the length of the first patella+tibia (Higgins et al. 2011). The growth ratio of an individual from previous instar (n_{i-1}) into current instar (n_i) was defined as the mass of n_i divided by the mass of n_{i-1} (e.g. Kleinteich and Schneider 2011).

Statistical analyses

Most of the data were not normally distributed, and were therefore log transformed to meet the assumption of homogeneity of variances. We compared developmental parameters

between treatments, sexes and sex \times treatment using General Linear Model (GLM), and applied the Bonferroni post hoc test. Although the adult mass data were normally distributed, they violated the assumption of Levene's test of homogeneity of variances ($p < 0.05$) despite various transformations. Therefore, we here used two GLMs for sex and treatment differences separately (Levene's tests of homogeneity of variances were then non-significant); we used Bonferroni tests to analyse differences between the three treatments. In the cases where significant effects of the treatments and sex (developmental time, mean inter-moult duration, mass and size at maturity) were detected, we further tested differences between treatments for males and females separately using GLMs; we used Bonferroni or Games-Howell post hoc tests. Here, all parameters met the assumption of Levene's test of homogeneity of variances.

We examined the effect of treatments on mass—transformed with $\log(x+1)$ —over development using repeated measures ANOVA with Bonferroni post hoc test. We tested the linear relationships between life-history trajectories for males and females separately using Pearson's correlations. The mortality and loss were compared between treatments using a Pearson's χ^2 . All tests, performed in SPSS Statistics 20, were two-tailed, and significance was set at $p < 0.05$.

Results

Treatment effects

Non-transformed data of growth and developmental parameters in *Nuctenea* spiders from different food treatments are given in Table 1. Spiders that received variable food quantities during development did not significantly differ in the number of instars until maturity and in the mean growth ratios (Table 2). However, they significantly differed in the mean inter-moult duration, total developmental time, adult patella+tibia I length and carapace width, as well as in the mass at maturity (Table 2). Spiders reared under HF matured earlier than spiders from both MF and LF ($p < 0.001$), and those from MF matured earlier than spiders from LF ($p < 0.001$). Similarly, spiders from different treatments, on average, spent variable periods in each instar; spiders from HF had shorter inter-moult durations than MF and LF spiders, and MF spiders had shorter inter-moult durations than LF spiders (HF:MF, $p = 0.001$; HF:LF, $p < 0.001$; MF:LF, $p < 0.001$). At adulthood, the spiders from HF had the longest patella+tibia I, whereas those from LF had the shortest legs (HF:MF, $p = 0.006$; HF:LF, $p < 0.001$; MF:LF, $p = 0.022$). The latter also reached maturity at significantly lower mass (HF:LF, $p < 0.001$; MF:LF, $p = 0.003$) and developed narrower carapaces (HF:LF, $p < 0.001$; MF:LF, $p < 0.003$). Spiders from HF and MF, however, did not

vary in either mass at maturity ($p = 0.698$) nor in carapace width ($p = 0.921$).

Inter-sex differences

We found sex differences in all measured developmental parameters, except in the number of instars (Table 2; Figs. 1b–f). Females exhibited higher growth ratios ($p < 0.001$), spent more time in each instar ($p < 0.001$) and needed more time to reach adulthood ($p < 0.001$) than did males. Accordingly, adult females were heavier than males ($p < 0.001$) and developed wider carapaces ($p < 0.001$) but shorter patella+tibia I ($p < 0.001$).

Intra-sex differences

The treatments somewhat differently affected males' and females' inter-moult durations and total developmental time: females from the three treatments significantly differed in total developmental time (Fig. 1c) and mean inter-moult durations (LF:MF, $p = 0.004$; LF:HF, $p < 0.001$; MF:HF, $p = 0.006$). Males from LF had the longest total developmental times and inter-moult durations (total developmental times, Fig. 1c; inter-moult durations, LF:MF, $p < 0.001$; LF:HF, $p < 0.001$); MF and HF males however had comparable developmental periods (total developmental times, Fig. 1c; inter-moult durations, $p = 1$). The adult size of both sexes was smallest in LF spiders, however, MF and HF spiders were of similar sizes (Fig. 1d, e). The mass at maturity differed between all treatments in males, but adult female mass differed only between LF and HF (Fig. 1f).

Detailed analyses revealed that males from different food supply treatments significantly varied in mass at moulting into given instars ($F_{19,2} = 4.744$, $p = 0.021$, Fig. 2b). While female mass at specific moulting was independent of food supply ($F_{41,2} = 2.378$, $p = 0.105$; Fig. 2a), the males from HF moulted at higher mass than males from LF and MF (LF:MF, $p = 1$; LF:HF, $p = 0.032$; MF:HF, $p = 0.125$; Fig. 2a, b).

Table 3 summarizes correlations between the developmental parameters. The mean inter-moult duration correlated positively with total developmental time and negatively to number of instars. In both sexes, the lower mean growth ratio related to a higher number of instars and longer development; however, the latter relationship was significant only in females. In males, but not in females, the spiders with longer inter-moult durations developed shorter legs and lower adult body mass. The higher growth ratio related to longer legs and wider carapaces in males.

Mortality and loss during the study

During the experiments, 20.48 % ($N = 34$) of individuals died; however, the occurrence of death was independent of the food

Table 1 Median (first, third quartile) values of non-transformed parameters in spiders from low (LF), medium (MF) and high food (HF) treatment during development

Parameter	Sex	Treatment		
		LF	MF	HF
Number of instars	♀	8 (7, 8.25)	7 (7, 8)	7 (7, 8)
	♂	7 (6,8)	7 (6, 8)	7 (6.5, 8)
Mean inter-moult duration (days)	♀	63.88 (58.18, 72.75)	48.2 (42, 53.8)	38.4 (35.21, 43.94)
	♂	64.5 (54.8, 73.14)	39.33 (33.11, 45.4)	35.75 (30.77, 42.85)
Total developmental time (days)	♀	390.5 (342.75, 466.25)	300 (282, 320)	237.5 (222.25, 261.5)
	♂	320 (307, 365)	239 (210.25, 257.25)	208 (193.5, 225)
Mean growth ratio	♀	1.82 (1.72, 2.25)	2 (1.8, 2.4)	2.09 (1.97, 2.3)
	♂	1.77 (1.68, 1.92)	1.95 (1.91, 2.19)	2.14 (1.95, 2.58)
Mass at maturity (g)	♀	0.09 (0.06, 0.1)	0.09 (0.09, 0.1)	0.11 (0.1, 0.12)
	♂	0.04 (0.04,0.05)	0.06 (0.05, 0.06)	0.07 (0.06, 0.07)
Length tibia+patella I (mm)	♀	4.6 (4.15, 5.17)	5.18 (5.05, 5.58)	5.6 (5.52, 5.78)
	♂	5.33 (5.02, 5.64)	6.14 (5.82, 6.42)	6.49 (6.04, 6.73)
Carapace width (mm)	♀	3.14 (2.73, 3.26)	3.82 (3.66, 4.01)	3.95 (3.72, 4.11)
	♂	2.75 (2.68, 2.88)	3.09 (2.93, 3.18)	3.28 (3.03, 3.41)

supply (*Pearson's* $\chi^2=0.549, df=2, N=166, p=0.743$). A very high percentage, 30.72 %, of spiders were lost during experiments ($N=51$). Significantly more spiders escaped/were lost from LF than from MF and HF (*Pearson's* $\chi^2=6.021, df=2, N=166, p=0.049$), which appears to be a consequence of longer periods of small spiderling sizes.

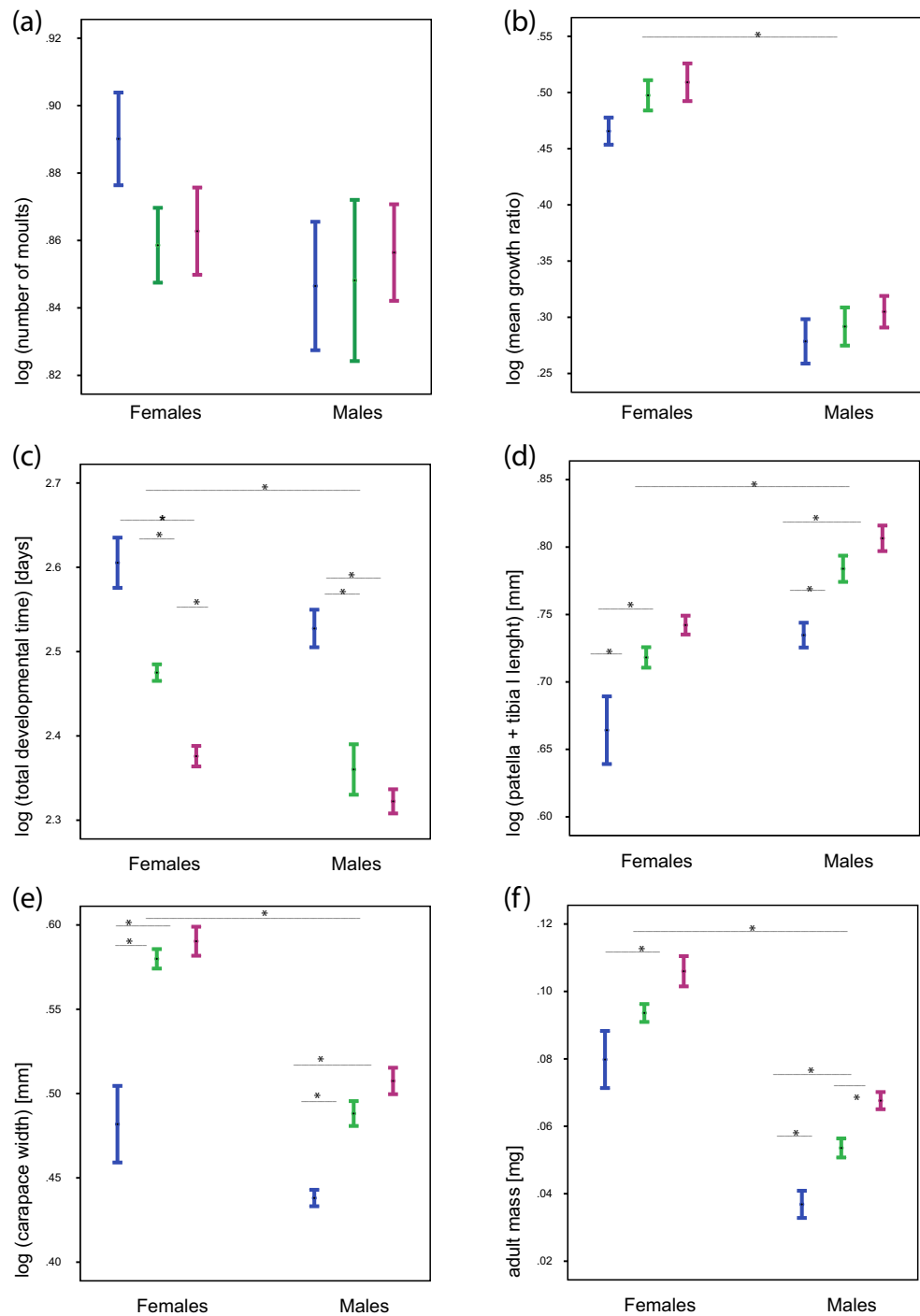
Discussion

The results of our study suggest that the partially synanthropic spider *Nuctenea umbratica* exhibits a canalized growth rate; growth ratios of individuals reared under different food quantity did not significantly vary. The spiders developed through

Table 2 The effects of treatments (high, medium and low food supply), sex, and treatment×sex on developmental parameters. Significant relationships are in italics

Developmental parameter	Independent factors	F	Significance
Number of instars	Treatment	0.404	0.669
	Sex	2.439	0.123
	Treatment×sex	0.800	0.453
Mean growth ratio	Treatment	2.121	0.127
	Sex	198.439	<0.001
	Treatment×sex	0.165	0.848
Mean inter-moult duration (days)	Treatment	42.234	<0.001
	Sex	47.447	<0.001
	Treatment×sex	1.002	0.372
Total developmental time (days)	Treatment	73.443	<0.001
	Sex	30.038	<0.001
	Treatment×sex	1.513	0.227
Length patella+tibia I (mm)	Treatment	18.691	<0.001
	Sex	51.038	<0.001
	Treatment×sex	0.031	0.969
Carapace width (mm)	Treatment	29.54	<0.001
	Sex	67.734	<0.001
	Treatment×sex	2.044	0.138
Mass at maturity (g)	Treatment	11.146	<0.001
	Sex	92.398	<0.001

Fig. 1 Growth and developmental parameters of spiders subjected to low food (LF), medium food (MF) and high food (HF) supply during development. *Error bars* means \pm SE of **a** number of instars; **b** mean growth ratios; **c** total developmental time (♀ : $p_{(\text{LF:MF})} = 0.005$, $p_{(\text{LF:HF})} < 0.001$, $p_{(\text{MF:HF})} < 0.001$; ♂ : $p_{(\text{LF:MF})} < 0.001$, $p_{(\text{LF:HF})} < 0.001$, $p_{(\text{MF:HF})} = 0.692$) **d** adult patella+tibia I length (♀ : $p_{(\text{LF:MF})} = 0.018$, $p_{(\text{LF:HF})} < 0.001$, $p_{(\text{MF:HF})} = 0.097$; ♂ : $p_{(\text{LF:MF})} = 0.018$, $p_{(\text{LF:HF})} < 0.001$, $p_{(\text{MF:HF})} = 0.303$); **e** adult carapace width (♀ : $p_{(\text{LF:MF})} < 0.001$, $p_{(\text{LF:HF})} < 0.001$, $p_{(\text{MF:HF})} = 1$; ♂ : $p_{(\text{LF:MF})} = 0.002$, $p_{(\text{LF:HF})} < 0.001$, $p_{(\text{MF:HF})} = 0.223$); and **f** mass at maturity (♀ : $p_{(\text{LF:MF})} = 0.305$, $p_{(\text{LF:HF})} = 0.04$, $p_{(\text{MF:HF})} = 0.061$; ♂ : $p_{(\text{LF:MF})} < 0.001$, $p_{(\text{LF:HF})} < 0.001$, $p_{(\text{MF:HF})} = 0.037$). *Asterisk* indicates significant differences ($p < 0.05$)



variable number of instars (i.e. 6–9; Fig. 1a) independently of sex and food availability. However, individuals from different feeding regimes needed different periods of time to reach adulthood, with more food availability

corresponding to earlier maturation. While adult sizes of spiders from medium and high food treatments exhibited comparable sizes, the spiders from low food treatment were the smallest.

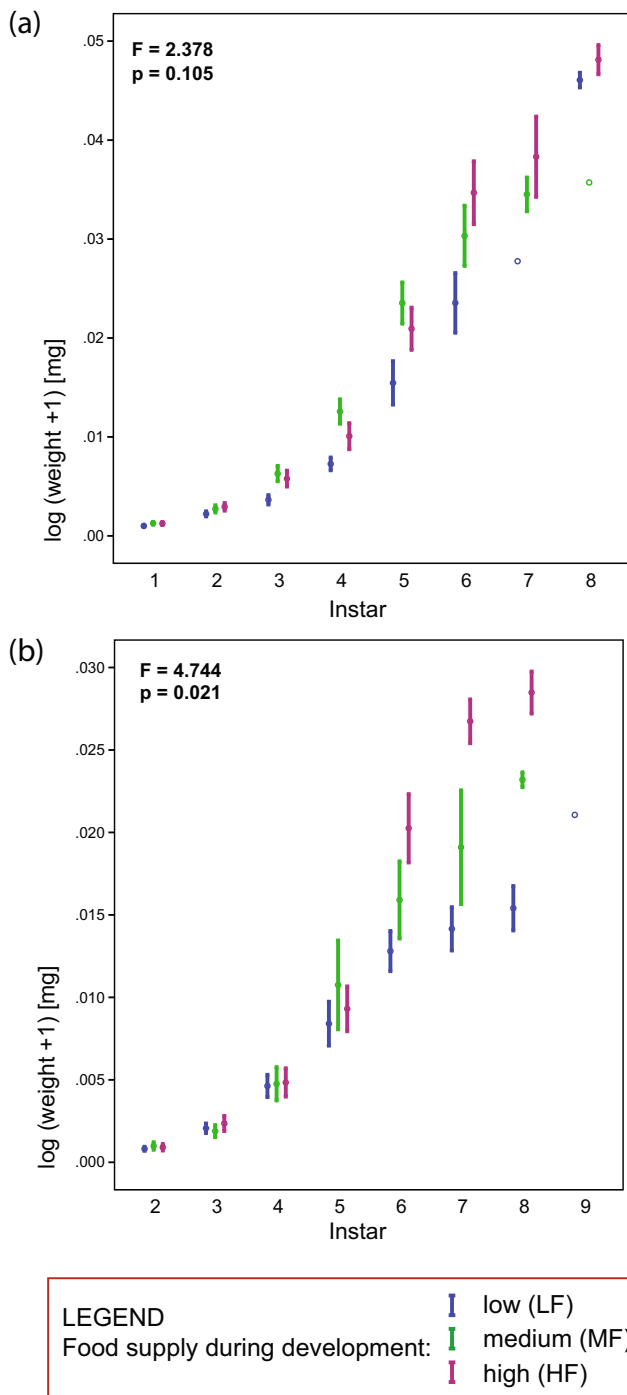


Fig. 2 Mass over development measured shortly after moulting in given instars. Error bars means \pm SE of mass in females (a) and males (b)

We found no significant variation in average growth ratios between spiders from the three different food treatments; however, MF and HF spiders matured at larger sizes than LF spiders. This seemingly contradictory data may result from individual differences and/or inter-relatedness between growth rate and number of instars. To examine the former explanation, we would have to test genetically related spiders originating from the same mother. The results on the

individual level (correlations) may be insightful: growth rate negatively correlated to instar numbers (the latter was independent of food supply, but highly variable; Fig. 1a). The above relationships suggest that an individual with, e.g. low growth rate could add moult(s), which may result in a body size comparable to individuals with relatively higher growth rates but lower number of instars. Furthermore, females may invest more nutrients into eggs than into measured body size proxies (carapace width and first leg length). This may explain why LF females had smaller size proxies but a comparable mass to MF females. Such growth and developmental patterns are likely adaptive, because in females mass relates to fecundity.

Developmental plasticity and exploitation of urban habitats

We contrast our results with those on *Larinioides* and *Zygiella*, two spiders that typically abound in highly urbanized areas and that show higher levels of growth and developmental plasticity (Mayntz et al. 2003; Kleinteich and Schneider 2011). *Larinioides* (*L. sclopetarius*) and *Zygiella* (*Z. x-notata*) decrease or increase numbers of instars and adjust growth ratio to food availability, and may also mature at significantly variable ages, sizes and mass (Mayntz et al. 2003; Kleinteich and Schneider 2011). While developmental rate seems to be plastic to some degree in *Nuctenea* as well, our prediction that *Nuctenea* would show more canalized growth compared with the two urbanites was met. The comparison between the three spider species that vary in their success of inhabiting urban areas lends support for our hypothesis that high growth and developmental plasticity in response to food resources could be a preadaptation to urban environments. We found no study on invertebrates comparing urban and non-urban species/populations growth and developmental plasticity; however, data from several studies suggest that plasticity may be important for coping with human-altered environment; in insects, plasticity in developmental trajectories depending on food supply during juvenile stage has been found mainly in economically important pests (reviewed in Esperk et al. 2007) and in the dipteran *Aedes aegypti*, a vector of human pathogens including dengue and yellow fever (Couret et al. 2014). Growth plasticity in response to diet has been shown in, e.g. *Manduca sexta*, a pest feeding on solanaceous plants (Kingsolver 2007).

Highly urbanized areas support unpredictably abundant resources. Insects, as the most important spider prey, may show high abundances near food wastes and may have prolonged season of activity (e.g. Kearney et al. 2010), but their numbers can fluctuate unpredictably. Insects are also abundant near city lights. Artificially lit urban habitats are commonly inhabited by *Zygiella* and *Larinioides* (Leborgne and Pasquet 1987; Heiling and Herberstein 1999; Kralj-Fišer and Schneider 2012), but not *Nuctenea* (this study). *Zygiella*

Table 3 Pearson's correlations between developmental parameters for females (in italics, above right) and males (in bold, below, left). Significant relationships are underlined

		DT	NI	ID	GR	MM	PTL	CW
DT	<i>r</i>		<i>0.139</i>	<i>0.786</i>	<i>-0.317</i>	<i>-0.111</i>	<i>-0.279</i>	<i>-0.068</i>
	<i>P</i>		<i>0.339</i>	<u><i><0.001</i></u>	<u><i>0.027</i></u>	<i>0.448</i>	<i>0.070</i>	<i>0.663</i>
	<i>N</i>		49	49	49	49	43	43
NI	<i>r</i>	0.165		<i>-0.340</i>	<i>-0.368</i>	<i>0.052</i>	<i>0.018</i>	<i>-0.048</i>
	<i>P</i>	0.366		<u><i>0.017</i></u>	<u><i>0.009</i></u>	<i>0.725</i>	<i>0.908</i>	<i>0.759</i>
	<i>N</i>	32		49	49	49	43	43
ID	<i>r</i>	0.737	-0.435		<i>0.002</i>	<i>-0.140</i>	<i>-0.238</i>	<i>-0.170</i>
	<i>P</i>	<u><0.001</u>	<u>0.013</u>		<i>0.988</i>	<i>0.337</i>	<i>0.124</i>	<i>0.276</i>
	<i>N</i>	32	32		49	49	43	43
GR	<i>r</i>	-0.289	-0.481	-0.016		<i>0.149</i>	<i>0.073</i>	<i>0.029</i>
	<i>P</i>	0.108	<u>0.005</u>	0.932		<i>0.308</i>	<i>0.643</i>	<i>0.854</i>
	<i>N</i>	32	32	32		49	43	43
MM	<i>r</i>	-0.526	0.222	-0.550	0.227			<i>0.872</i>
	<i>P</i>	<u>0.002</u>	0.223	<u>0.001</u>	0.212			<u><i><0.001</i></u>
	<i>N</i>	32	32	32	32			43
PTL	<i>r</i>	-0.520	-0.030	-0.473	0.415	0.595		<i>0.631</i>
	<i>P</i>	<u>0.009</u>	0.988	<u>0.020</u>	<u>0.044</u>	<u>0.002</u>		<u><i><0.001</i></u>
	<i>N</i>	24	24	24	24	24		43
CW	<i>r</i>	-0.513	0.163	-0.541	0.550	0.848	0.738	
	<i>P</i>	<u>0.010</u>	<u>0.446</u>	<u>0.006</u>	<u>0.005</u>	<u><0.001</u>	<u><0.001</u>	
	<i>N</i>	24	24	24	24	24	24	

DT total developmental time, NI number of instars, ID mean inter-moult duration, GR mean growth ratio, MM mass at maturity, PTL adult patella+tibia I length, CW adult carapace width

response to increased prey availability is highly plastic: they mature earlier and produce more and heavier eggs (Spiller 1992). They develop in cca. 160 days under unlimited food accessibility (Mayntz et al. 2003), and might potentially have two generations per year in favourable conditions. *Larinioides* fed with high numbers of prey develop even faster, in approximately 60 days (Kleinteich and Schneider 2011), and may have up to four generations per year in laboratory conditions (Schneider personal observation). Accelerated growth, earlier maturation and reproduction under high prey abundance were proposed to enable the bridge spider to successfully proliferate in urban habitats (Kleinteich and Schneider 2011). In successful urban spiders such as *Zygiella* and *Larinioides*, growth and developmental plasticity likely facilitates and, in combination with high food availability, results in shorter generation turnover (intrinsic rate of population) and increased fitness (net reproductive rate), and consequently, in rapid population growth.

In comparison with *Zygiella* and *Larinioides*, the development of *Nuctenea* is much slower and does not become accelerated with abundant and constant food supply, with artificially longer light periods, nor with increased winter temperature (i.e. the laboratory conditions in our study). In the laboratory conditions, well-fed spiderlings that had

hatched in November/December, matured only in July to October (or in roughly 240 days in females; 210 days in males; Table 1), which is not before their natural mating season in the field (Nentwig et al. 2014). However, the determined growth ratio precluded timely development of spiders with a highly restricted food supply (LF). Spiders from LF did not exhibit higher mortality; however, females and males needed, on average, 390 and 320 days, respectively, from hatching to maturation and were relatively smaller as adults (Table 1). We believe their long development and inferior size would have severe fitness consequences in the field. Juvenile females would miss the mating opportunities during the main reproductive season from June to October. Even if they did mate, their reproductive output, which in spiders generally relates to body mass (Suter 1990; Higgins 1992; Head 1995), would be reduced compared with well-fed females. Males maturing late in reproductive season would also exhibit low mating success as their small size would be disadvantageous in male–male contests (Christenson and Goist 1979; Vollrath 1980; Foellmer and Fairbairn 2005). Therefore, we propose that *Nuctenea* individuals may fail to survive and reproduce in urban environments with low/sporadic prey availability. We suggest that their canalized growth ratio and slow generation turn-over (with up to one generation per year) precludes their

success in the stochastic urban environments where they face competitors with greater developmental plasticity and faster generation turn-over such as *Larinioides* and *Zygiella*.

While *Nuctenea* exhibited limited plasticity in the growth ratio, their total developmental time highly depended on food abundance. In HF treatment, spiders spent less time in an instar and matured earlier than those from LF treatment. Despite disadvantages described above, the MF spiders reach adulthood at size and mass allowing them to optimize their fitness in given environmental conditions. Females from restricted food supply (MF) needed on average 300 days to adulthood, and thus matured in the late reproductive season; however, their body size and mass was not significantly lower from HF females. Consequently, they might have fewer mating opportunities in the field, yet, when mated, their reproductive output should be comparable with HF females, which in our study, received double amounts of food. Therefore, it is plausible to expect that females with adequate food supply (MF) would be able to minimize their fitness consequences compared with well-fed females. On the other hand, males from MF matured over similar periods than HF males, however, at the smaller mass. Such sex variation in developmental plasticity is likely adaptive; while males need to mature timely, females need to increase their fecundity.

Intra-sex differences

Nuctenea spiders exhibited sex differences in growth and developmental trajectories: males exhibited lower growth ratios and shorter inter-moult durations, but matured earlier and reached lower mass and narrower carapaces, but longer first legs than females. These differences are in accordance with other moderately sexually sized dimorphic spiders with protandric mating system (e.g. Kralj-Fišer et al. 2013). Food availability affected developmental times in both sexes. However, females moulted into a given instar at a specific mass independently of the food treatment, whereas males' moulting pattern shifted to lower mass when food was restricted. These results suggest that males exhibit more plastic development than females. Similarly, a study on the Mediterranean tarantula (*Lycosa tarantula*) found a more canalized development to adult size in females than in males (Fernández-Montraveta and Moya-Laraño 2007). Our data suggest that females—but not males—had rather fixed critical mass to moult into the next instar and to reach maturity (cca. 0.06 g; Table 1, Fig. 1). This sex difference in plasticity is logical since female adult mass strongly relates to fecundity, affecting her fitness (Suter 1990; Higgins 1992; Head 1995). Adult males, on the other hand, are more time-restricted; they are usually not found during winter times in the field and such adjustments likely enable them to catch up to the reproductive season relatively independently of the mass and size at maturity (when compared to females). Such data are in accordance

with scramble competition acting on males in female-biased sexually size dimorphic species (Andersson 1994). Sex differences in plasticity of mechanisms affecting body size in response to diet have been also found in some sexually sized dimorphic insects, e.g. the hawkmoth, *Manduca sexta* and Australian fly, *Telostylinus angusticollis* (Bonduriansky 2007) suggesting complex sex-specific responses to environmental variation.

The restriction of food treatments was similar in the three compared spider studies (Mayntz et al. 2003; Kleinteich and Schneider 2011), except that in the HF treatment, *Zygiella* and *Larinioides* received unlimited food (Mayntz et al. 2003; Kleinteich and Schneider 2011), but *Nuctenea* were restricted to two flies twice a week. While this could have biased our HF data, we find it unlikely because the growth rate and instar number did not differ between LF and MF treatments, and because females moulted into specific instars at similar masses regardless of food conditions. Therefore, a rather canalized growth rate and plastic inter-moult duration would also likely be detected if the HF spiders were fed ad libitum.

Conclusions

Nuctenea umbratica exhibits elements of both canalization and plasticity in growth and developmental trajectories. While they are unconstrained in developmental time (in the laboratory) enabling them to achieve maximal mass and size—main fitness proxies—in given conditions, the relatively fixed growth ratio and long generation turn-over may be the reasons for their relatively lower success in the urban environments when compared with urban achievers such as *Zygiella* and *Larinioides*. In *Nuctenea*, the increased terminal female sizes affecting the net reproductive rate (R) likely counter-balance the slow generation turn-over, leading to stable population size. In *Zygiella* and *Larinioides*, increased R and short generation time relate to a high intrinsic rate of population growth in favourable conditions (Kingsolver and Huey 2008), and to a high urban colonization success.

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