

Ecotypic differentiation between urban and rural populations of the grasshopper *Chorthippus brunneus* relative to climate and habitat fragmentation

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Abstract Urbanization alters environmental conditions in multiple ways and offers an ecological or evolutionary challenge for organisms to cope with. Urban areas typically have a warmer climate and strongly fragmented herbaceous vegetation; the urban landscape matrix is often assumed to be hostile for many organisms. Here, we addressed the issue of evolutionary differentiation between urban and rural populations of an ectotherm insect, the grasshopper *Chorthippus brunneus*. We compared mobility-related morphology and climate-related life history traits measured on the first generation offspring of grasshoppers from urban and rural populations reared in a common garden laboratory experiment. We predicted (1) the urban phenotype to be more mobile (i.e., lower mass allocation to the abdomen, longer relative femur and wing lengths) than the rural phenotype; (2) the urban phenotype to be more warm adapted (e.g., higher female body mass); and (3) further evidence of local adaptation in the form of significant interaction effects between landscape of origin and breeding temperature. Both males and females of urban origin had significantly longer relative femur and wing lengths and lower mass allocation to the abdomen (i.e., higher investment in thorax and flight muscles) relative to individuals of rural origin. The results were overall significant but small (2–4%). Body mass and larval growth rate were much higher (+10%) in females of urban origin. For the life history traits, we did not find evidence for significant

interaction effects between the landscape of origin and the two breeding temperatures. Our results point to ecotypic differentiation with urbanization for mobility-related morphology and climate-related life history traits. We argue that the warmer urban environment has an indirect effect through longer growth season rather than direct effects on the development.

Keywords Anthropogenic landscapes · Contemporary evolution · Dispersal · Thermoregulation

Introduction

Urbanization is a worldwide phenomenon (Pickett et al. 2001). Typically, conservation biologists have focused on the associated loss and degradation of rural and natural habitats, but there has been recent interest in the novel value of these transformed environments. Urban areas—cities in particular—are typified by higher levels of chemical and physical pollution, warmer local climatic conditions and a higher prevalence of exotic species (Pickett et al. 2001; McKinney 2002).

The many heat-absorbing surfaces of urban areas create relatively warm environments compared to rural or natural environments at the same latitude or altitude (“urban heat island effect”; Souch and Grimmond 2006). Urban climate may directly affect behaviors and habitat-use of organisms (e.g., Parris and Hazell 2005), particularly so in ectotherms. But it may also affect organisms in an indirect way through, for example, temperature-related changes in phenology and the available time for reproduction (e.g., Partecke et al. 2004; Neil and Wu 2006). Urban areas typically have small and strongly fragmented habitat patches which affect local extinction and turnover rates

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(e.g., Husté and Boulinier 2007). The habitat used by organisms in urban areas may also differ in quality from the corresponding habitat in other landscapes. Moreover, urban areas have a very different landscape matrix between habitat patches resulting most often in lower functional connectivity (e.g., Niemela 1999; Verbeylen et al. 2003).

Urban areas may, hence, impose ecological and evolutionary filters to the pool of species able to cope with these environmental conditions (e.g., Shochat et al. 2006; Kark et al. 2007). At the intra-specific level, urban environments may select for different trait values or influence trait expression compared to natural environments (Shochat et al. 2006). Recent studies have, for example, shown differential adaptive responses of urban versus rural bird populations (e.g., Slabbekoorn and Ripmeester 2008; Evans et al. 2009). Some patterns suggest evolutionary change through genetic adaptation to urban conditions, but in the majority of the studies, genetic adaptation could not be distinguished from phenotypic plasticity. At least in some cases, differentiation can also be the result of founder effects and genetic drift (Ditchkoff et al. 2006).

Here, we tested for adaptive ecotypic differences between urban and rural populations of an ectotherm, the grasshopper *Chorthippus brunneus*. We focus on life history traits known to respond to temperature along climatic clines and on movement-related morphological traits predicted to respond to habitat fragmentation. Predictions were tested with a common garden breeding approach in the laboratory. The traits were measured on the first generation offspring from urban and rural populations of two different regions in Belgium reared under high and low temperature conditions.

C. brunneus is a thermophilous species of short turf grassland; it is usually found in early seral vegetation stages (Detzel 1998). In cities, this vegetation is typically expected to occur in a highly dispersed manner in a number of small to intermediately sized patches. The spatio-temporal distribution of such grassland patches in an urban environment is also expected to be highly dynamic. As a result, the population system is likely to be metapopulation-like with a high turn-over rate. Hence, more mobile individuals are more likely to found new populations. Movement is frequently hypothesized to have evolved as a way of coping with ephemerality of populations (Dingle and Holyoak 2001). Hence, we predict that individuals of urban populations are more dispersive compared to rural individuals. Therefore, we compare relative investment in adult morphological traits that are functionally significant for movement. We predict longer relative femur and wing sizes and also lower relative abdomen mass (i.e., higher allocation to thorax and flight muscles) in grasshoppers of urban population origin.

Several studies on grasshoppers, including *C. brunneus*, have tested evolutionary responses to climate along latitudinal or altitudinal gradients for life history traits. Females are heavier in warmer regions (Tregenza et al. 2000; Berner and Blanckenhorn 2006; Fielding and Defoliart 2007) or in regions with mild winters (Telfer and Hassall 1999). Heavier weight is often associated with longer development time that is sometimes compounded by lower growth rate (Hatle et al. 2002; Berner and Blanckenhorn 2006; Fielding and Defoliart 2007). Taking into account the warmer conditions of urban areas, we predict that urban populations have life history traits similar to more southern (or lower altitude) conditions compared to rural populations at the same latitude or altitude.

As we reared the individuals in two different breeding temperatures, we were also able to explore interaction effects between the landscape of origin and temperature treatment (e.g., Karlsson and Van Dyck 2005). One may predict urban phenotypes to be more warm adapted than rural phenotypes, and hence there could be stronger differences between the phenotypes that developed under low and high temperatures in urban populations compared to rural populations (i.e., landscape of origin \times temperature interaction). We will discuss the differences in morphology and life history between the populations of different landscape of origin within the context of (adaptive) responses to urban environments.

Materials and methods

Study species

Chorthippus brunneus (Thunberg, 1815) (Orthoptera, Acrididae) is a xerothermophilous species of pioneer vegetations, but it is able to live in a variety of open vegetation due to its developmental and reproductive plasticity and efficient thermoregulation behavior (Detzel 1998; Willott and Hassall 1998). As pioneer species, it has good dispersal abilities (Richards and Waloff 1954; Detzel 1998; Picaud and Petit 2007). There is one generation a year with adults from late June to early August. Egg pods (4–16 eggs) are laid in the ground and hatch in May of the next year after obligate winter diapause.

Sampled populations

In August 2006, we collected 20 males and 20 females in each of 6 urban and 6 rural sites in Belgium. To allow generalization, we studied urban and rural sites in two different regions. The first region was in central Belgium with Brussels as the urban zone (1 million citizens; 50.84°N, 4.35°E), and Louvain-la-Neuve as the rural zone

(50.66°N, 4.61°E). The second region was in northern Belgium with Antwerp as the urban zone (550,000 citizens; 51.21°N, 4.41°E) and Herentals as the rural zone (51.17°N, 4.83°E). In each zone, we sampled 3 areas (populations) with dry, open grass vegetation that were >1 km from each other. The distance between the urban and rural zone is about 30 km for both regions. The presence of *C. brunneus* in the studied zones has been confirmed for at least several decades.

Laboratory breeding

For the breeding protocol, we closely followed Kelly-Stebbins and Hewitt (1972). Grasshoppers were kept in cylindrical cages (diameter 15 cm, height 25 cm) in a climate room (light:dark 14:10 h) at constant ambient temperature (see below). In contrast with Kelly-Stebbins and Hewitt (1972), no additional bulbs were provided to reduce the impact of behavioral thermoregulation by extensive basking. The grasshoppers had access ad libitum to fresh grass (mixture dominated by *Lolium perenne*). Freshly cut grass was placed in a bottle of water in the cage, and refreshed every 2 (or 3) days. A recipient with sterile dry sand was provided for egg laying. Every 2 (or 3) days, we collected the egg pods and placed them in Petri dishes filled with 10% humidified sand. Egg pods were conserved for 3–4 weeks at room temperature allowing embryonic development up to the diapause stage. Next, we placed the Petri dishes for 3 months at 4°C to break diapause. Egg pods were then dissected, and the eggs were placed on a hatching device (Kelly-Stebbins and Hewitt 1972).

Five couples from each population were isolated in individual cages. When a female died, a new strain was initiated by isolating a new female. All the adults of the parental generation were kept at 30°C. Three females with at least 10 egg pods were randomly chosen from each population of the parental generation to initiate the F1 generation. The eggs were placed at 30°C after dissection of the egg pods. Most eggs hatched on the same day and the nymphs were placed in one cage per family ($n = 36$ families). After 12 days, half the nymphs of each family were assigned to either the high temperature treatment (i.e., 35°C) or the low temperature treatment (i.e., 27°C), and the cage density was recorded. The high temperature approaches to optimal temperature (relative to fitness), whereas the low temperature is clearly suboptimal (Willott and Hassall 1998).

Cages were checked daily for newly eclosed adults. New adults were weighed (Denver Instruments balance APX-200, accuracy ± 0.1 mg) and individually marked. Day of death was recorded and individuals were stored for morphometric measurements.

Morphological traits

We measured wing length, femur length and abdomen mass at death. To control for body size and mass, we also measured pronotum length and total body mass at death. Lengths were measured by stereo-microscope with a reticulated ocular (accuracy ± 0.06 mm). We measured both left and right wing and femur. We used the mean values of both left and right sides for wing and femur lengths. As wings often had wing wear, we did not measure total wing length, but the distance between the wing base and the intersection between the sub-costal and costal veins. This measure correlated strongly with total wing length ($R^2 = 0.94$, $n = 20$ intact males and 20 intact females). As overall size index, we used pronotum length. Hence, we can express wing length and femur length relative to pronotum length.

Before weighing, individuals were dried to constant mass during 24 h at 60°C. Body mass and abdomen mass (after careful removing from the thorax) were measured with a high precision balance (accuracy ± 0.1 mg). Allocation to abdomen was expressed relative to total body mass.

Life history traits

We recorded four life-history traits: (1) larval development time (i.e., the number of days between egg hatching and adult eclosion); (2) adult lifespan (i.e., the number of days between adult eclosion and death); (3) fresh adult body mass at eclosion; and (4) growth rate (i.e., adult fresh body mass at eclosion/larval development time).

We have also measured the number of eggs per egg pod and the average mass of the eggs for each egg pod. We have weighed only the eggs with a well-developed embryo by means of a high precision balance (Mettler Toledo MT5, accuracy ± 0.001 mg). Almost no eggs from the females reared at 27°C showed well-developed embryos. Therefore, this part was limited to the 35°C treatment.

Statistical analysis

We used linear mixed models to estimate the effect of the landscape of origin (urban or rural), temperature treatment 35 or 27°C) and their interaction effect on movement-related morphology and life history traits. They were used as fixed effects. Population and family (nested in population) were included as random effects to take into account the statistical dependence of the individuals at the family and population level. We are mainly interested in the fixed effects, and random effects are mainly considered to adjust statistical estimation; random effect estimates are not shown in the tables. Density in the cages at the beginning of

the experiment (separation into two temperature treatments) was also included in the models as a fixed covariate.

For wing length and femur length, we included pronotum length as a covariate to control for overall body size. Hence, this represents an estimate of relative wing length and relative femur length. We included total dry body mass for the analysis of abdomen mass. Covariates and the density in the cage were centered to their mean. Models were fitted separately for males and females.

The fixed effects were tested with likelihood ratio tests by comparing nested models estimated by maximum likelihood (Pinheiro and Bates 2000). We respected marginality rules, as models without one main effect were always compared with the full model without the interaction containing this main effect. We used R (version 2.9) and the lme4 R package for all analyses.

Results

Totals of 379 females and 310 males reached the adult stage. Tables 1, 2 and 3 summarize the results of the mixed models testing movement-related morphology, life history traits and egg traits relative to landscape of origin, temperature treatment and the interaction effect.

Adult morphology

The temperature treatment did not affect relative wing and femur lengths, or relative abdomen mass allocation in females (Table 1; Fig. 1). Males had longer relative femurs under optimal temperature treatment compared to suboptimal treatment (+2.1%, $P = 0.007$) and body mass allocation to the abdomen was lower (−2.8%, $P = 0.018$).

Both males and females of urban population origin differed in morphology from conspecifics of rural populations, independent of the temperature treatment. Urban origin grasshoppers had longer relative wings (+2.4%, $P = 0.046$ for males, and +2.6%, $P = 0.011$ for females), longer relative femurs (+2.8%, $P = 0.012$ for males, and +2.9%, $P = 0.001$ for females), and lower relative allocation to the abdomen (−3.7%, $P = 0.044$ for males, −3.6%, $P = 0.006$ for females) compared to rural origin grasshoppers (Fig. 1).

In cages with higher initial densities (mean = 16.2, SD = 9.67, range = 2–39 individuals/cage), femur length was slightly shorter relatively to body size (−1.7%, $P = 0.001$ for females and −2.1%, $P = 0.002$ for males and for cage densities of 10 individuals above the mean density), wing length was shorter relatively to body size for males only (−2.2%, $P = 0.003$ for cage densities of 10 individuals above the mean density) and body mass allocation to the abdomen at death was higher for females

Table 1 Summary of the fixed variables from mixed models for movement-related morphological traits (corrected for cage density) in adult female (F) and male (M) grasshoppers *Chorthippus brunneus* relative to breeding temperature (27 vs. 35°C), landscape of origin (urban vs. rural) and the interaction effect

Sex	Trait	Intercept			Density			Covariable			Temperature (35°C)			Landscape (urban)			Landscape × temp.					
		Coeff.	SE	P	Coeff.	SE	P	Signif.	Coeff.	SE	P	Signif.	Coeff.	SE	P	Signif.	Coeff.	SE	P			
F	Dry abdomen mass (mg)	14.79	0.24	0.05	0.01	0.000	***	0.61	0.01	0.000	***	−0.40	0.28	0.058	(*)	−0.55	0.34	0.006	**	0.05	0.39	0.906
	Femur length (mm)	40.33	0.28	−0.07	0.02	0.001	***	2.54	0.11	0.000	***	−0.11	0.28	0.962		1.08	0.39	0.001	**	0.20	0.39	0.595
	Wing length (mm)	42.35	0.34	−0.03	0.02	0.174		2.18	0.13	0.000	***	−0.13	0.33	0.136		1.28	0.47	0.011	*	−0.40	0.45	0.360
M	Dry abdomen mass (mg)	5.99	0.09	0.00	0.01	0.857		0.38	0.01	0.000	***	−0.17	0.10	0.018	*	−0.23	0.13	0.044	*	0.02	0.14	0.905
	Femur length (mm)	33.22	0.29	−0.07	0.02	0.002	**	1.60	0.22	0.000	***	0.83	0.36	0.007	**	1.05	0.42	0.012	*	−0.26	0.53	0.594
	Wing length (mm)	36.4	0.35	−0.08	0.02	0.003	**	1.18	0.21	0.000	***	0.19	0.34	0.287		0.81	0.49	0.046	*	0.16	0.49	0.778

Dry body mass was used as covariate for dry abdomen mass and pronotum length for wing and femur lengths. Model structure takes into account family and population as random effects (details not shown; see “Materials and methods”).

P values are from likelihood ratio tests: (*) $P < 0.1$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Table 2 Summary for the fixed variables from mixed models for life history traits in adult females (F) and males (M) relative to breeding temperature (27 vs. 35°C), landscape of origin (urban vs. rural) and the interaction effect (corrected for cage density)

Sex	Trait	Intercept			Density			Temperature (35°C)			Landscape (urban)			Landscape × temp.			
		Coeff.	SE	P	Coeff.	SE	Signif.	Coeff.	SE	P	Coeff.	SE	Signif.	Coeff.	SE	P	
F	Adult lifespan (days)	29.78	2.63	0.29	0.14	0.041	*	-3.26	2.48	0.004	**	4.12	3.67	0.449	-3.48	3.47	0.299
	Growth rate (mg/day)	3.06	0.16	-0.05	0.01	0.000	***	1.56	0.15	0.000	***	0.44	0.22	0.026	-0.04	0.21	0.869
	Body mass at eclosion (mg)	105.06	3.54	-1.33	0.23	0.000	***	14.1	3.6	0.000	***	15.64	4.95	0.003	-4.55	5.03	0.373
	Larval development time (days)	35.09	0.55	0.07	0.04	0.036	*	-9.02	0.55	0.000	***	0.99	0.77	0.373	-0.82	0.77	0.280
M	Adult lifespan (days)	30.63	2.82	-0.08	0.17	0.602		-1.17	2.99	0.112		4.47	4.11	0.553	-5.44	4.47	0.219
	Growth rate (mg/day)	2.31	0.1	-0.04	0.01	0.000	***	0.79	0.08	0.000	***	0.05	0.14	0.257	0.16	0.12	0.216
	Body mass at eclosion (mg)	71.79	1.86	-0.67	0.11	0.000	***	3.21	1.73	0.000	***	1.04	2.69	0.179	3.91	2.57	0.143
	Larval development time (days)	32.14	0.59	0.14	0.03	0.000	***	-7.74	0.41	0.000	***	-0.28	0.85	0.776	0.21	0.61	0.726

Model structure takes into account family and population as random effects (details not shown; see “Materials and methods”) P values are from likelihood ratio tests: * P < 0.05, ** P < 0.01, *** P < 0.001

Table 3 Summary of the fixed variables of the mixed models for egg traits relative to the landscape of origin (urban vs. rural)

Trait	Intercept		Landscape (urban)		P	Signif.
	Coeff.	SE	Coeff.	SE		
Eggs mass (mg)	5.18	0.14	0.37	0.19	0.052	(*)
No. of eggs per eggpod	6.98	0.31	0.54	0.43	0.198	

Model structure takes into account family and population as random effects (details not shown; see “Materials and methods”)

P values are from likelihood ratio tests: (*) P < 0.1

(+3.4%, P < 0.001 for cage densities of 10 individuals above the mean density). The initial mean density was very similar between cages with urban and rural origin families (mean = 16.5 and 15.8, respectively).

Life history traits

The temperature treatment had a strong and highly significant effect on most life history traits in males and females (Table 2). Body mass at eclosion and growth rate were higher at optimal compared to suboptimal temperature, particularly for females. Larval development time was significantly shorter at 35°C (males: -7.6 days, females: -9.4 days). Adult lifespan was significantly shorter in females at 35°C (-5 days), but not in males.

Landscape of origin did not affect the studied life history traits of males, but urban origin females grew faster than rural females (+11.5%, P = 0.026) and they were heavier at eclosion than rural females (+12.6%, P = 0.003), independent of breeding temperature (Fig. 2).

Reaction norms of urban populations were highly similar to those of rural populations (i.e., no significant landscape of origin × breeding temperature interactions; all P values > 0.1).

At optimal ambient temperature, egg mass (average mass of single eggs) of urban origin females tended to be heavier than egg mass of rural origin females (+7.1%, P = 0.052, see Table 3).

Density had a highly significant adverse effect on the life-history traits. With increasing density, body mass at eclosion and growth rate did decrease and larval development time became longer. For females only, adult lifespan was however longer at higher densities (+9.7%, P = 0.041 for a cage density of 10 individuals above the mean density).

Discussion

Our breeding experiment with replicate urban and rural populations of the grasshopper *C. brunneus* provided

Fig. 1 Predicted values (\pm SE) for three movement-related morphological traits (wing length, femur length and dry abdomen mass) of female (a, c, e) and male (b, d, f) grasshoppers *Chorthippus brunneus* relative to landscape of origin (urban vs. rural) for high (35°C) and low (27°C) breeding temperatures. Urban solid symbols, continuous line. Rural open symbols, dashed line. Estimates are corrected for cage densities. Wing and femur lengths are corrected for pronotum length and abdomen mass is corrected for total body mass

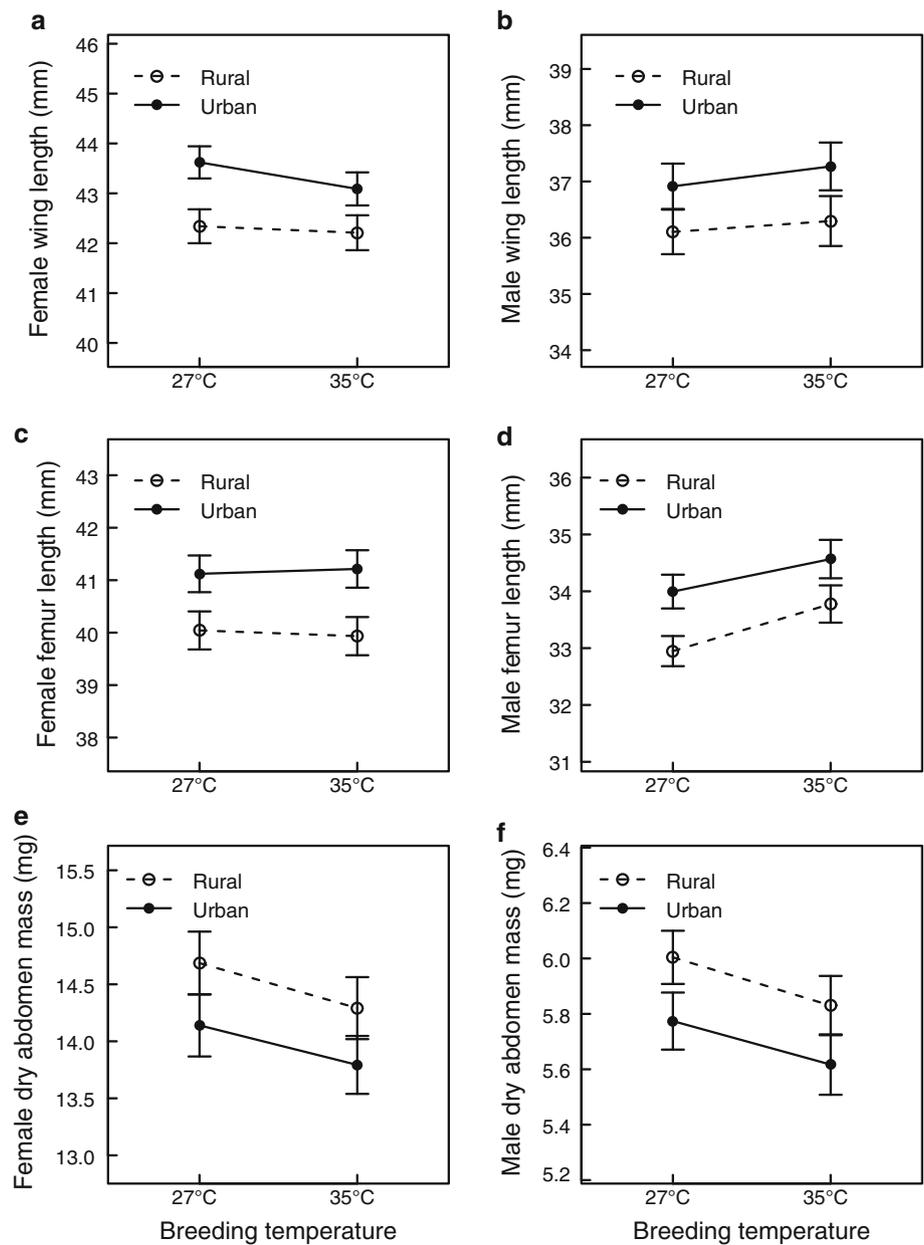
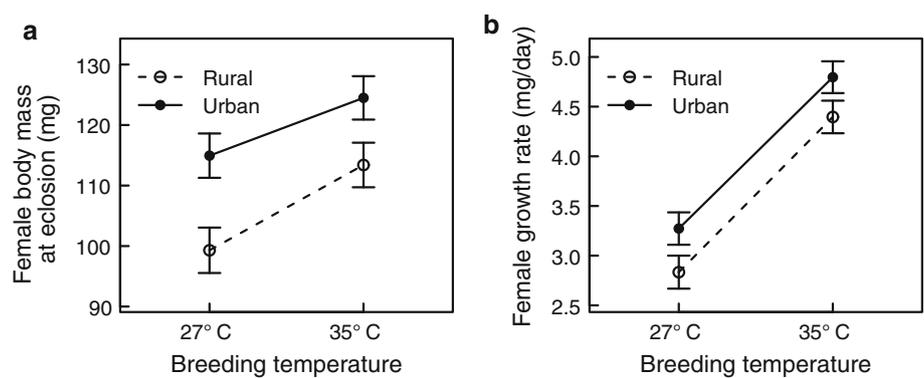


Fig. 2 Predicted values (\pm SE) of female body mass (a) and growth rate (b) relative to landscape of origin (urban vs. rural) for high (35°C) and low (27°C) breeding temperatures. Urban solid symbols, continuous line. Rural open symbols, dashed line. Estimates are corrected for cage densities



support for the hypotheses on adaptive ecotypic differentiation for movement-related morphology and life history traits. Morphological differences were generally significant, but rather small in both males and females. Predicted life history differences based on climate-related effects were well pronounced in females. However, urban and rural populations did not respond differently in terms of life history traits or morphological traits to the two temperature treatments (i.e., no landscape \times temperature treatment interaction effect).

The fact that we worked under common garden conditions on the first generation of several grasshoppers populations coming from two different regions suggests heritable effects. This can be the result of genetic adaptation to urban environment, but can also be caused by other heritable effects like maternal effects. In this study system, the most likely maternal effect could be via egg size influenced by the age of the female (Cherrill 2002), or by the temperature (Hassall et al. 2006) experienced by the parental generation on the field before it was placed under controlled laboratory conditions. We have no data about egg size of the parental generation, but we showed a tendency towards a difference in egg size between urban and rural populations for the F1 generation that was bred under common garden conditions. Hence, a difference in egg size could itself be the result of ecotypic differentiation, and we cannot exclude such, still poorly understood, maternal effects. However, maternal effects are currently often viewed as an important mechanism in evolutionary processes, and, hence, they are no longer considered as evolutionary noise as was done until recently (Badyaev 2009). The differentiation of maternal effects from genetically based differences is extremely difficult. Maternal effects can be observed during several generations (Benton et al. 2008), and breeding several generations under laboratory conditions may lead to confounding effects of artificial selection. Genetically based differentiation between urban and rural populations could also be due to genetic drift or stochastic differences of the colonists (founder effect; Yeh 2004; Evans et al. 2009). This is, however, unlikely to play a significant role here as we found consistent effects using several populations from two different regions. Although further research on the genetic mechanisms behind the observed pattern is now warranted, the differences in ecologically relevant differences in morphology and life history between urban and rural populations were as predicted.

The morphological differences largely matched the predictions based on the hypothesis of selection for increased mobility in urban landscapes. Wing length relative to thorax length and relative body mass allocation to the thorax are often used as an indicator of dispersal ability in insects (e.g., Kolliker-Ott et al. 2004; Gibb et al. 2006). However, the

functional significance for movement and dispersal, in particular, is typically assumed but rarely tested. Morphological traits have been found to show evolutionary responses in insect populations of fragmented versus continuous landscapes, and core versus range margin populations (e.g., Thomas et al. 1998; Hughes et al. 2007; Hassall et al. 2009). Despite the relatively high number of individuals we used—and hence the high statistical power—the morphological differences were quite small (2–4%). The same is true for the cited studies on other insects. It strengthens the need for further functional testing of such differences. *C. brunneus* has also been cited as a pioneer and mobile species (Detzel 1998; Picaud and Petit 2007) which makes it potentially pre-adapted to fragmented urban environments. The small but significant morphological differences should be further tested in this context.

The higher degree of habitat fragmentation in urban landscapes compared to rural landscapes could select for higher movement performances and, hence, more ‘mobile’ morphologies. However, ambient temperature may increase the frequency of long distance dispersal events in grasshoppers (Walters et al. 2006). Hence, even in the absence of functional differentiation of the mobility-related morphology, the warmer urban climate may facilitate movements via a change in the functional connectivity of the landscape. Thermal aspects are, however, not the only differences between the urban and the rural landscape matrices. The study of landscape matrix effects on *C. brunneus* movements needs further work. Moreover, it would also be interesting to do additional tests at higher temperatures as interactions may only be evident at temperatures above 35°C.

Contrary to the small morphological differences, we found strong differences in life history. Females of urban population origin were >10% heavier at eclosion than females of rural population origin. Grasshopper body size is of great biological significance as female body mass is typically related to several fecundity traits: number of eggs per egg pod, total number of egg pods, and female lifespan (Richards and Waloff 1954; Walters and Hassall 2006). Selection of higher female body mass in populations from warmer environments has been observed in many Acrididae species and along different climatic gradients (Telfer and Hassall 1999; Tregenza et al. 2000; Berner and Blanckenhorn 2006; Fielding and Defoliart 2007). Grasshoppers are well-known exceptions to Bergmann’s rule (Walters and Hassall 2006). Warm urban climate is, therefore, a good candidate to explain the observed body mass differences in our study, although we cannot exclude other mechanisms at this stage. In particular, food quality (e.g., Grayson and Hassall 1985) and density (this study) may induce plastic response of life history traits that could differ between urban and rural landscapes. Hence, other

correlated environmental factors could also act as selective pressures leading to the observed ecotypic differentiation in our study as in the previously cited studies along climatic and altitudinal gradients.

Warm climate populations can develop during a longer time period as they are less time-stressed and they can reach a higher body mass with a constant growth rate (Berner and Blanckenhorn 2006). However, we did not find any differences between the populations for development time, while urban populations had higher growth rates. The relationships between climate, development time, growth rate and body mass can be quite complex. Telfer and Hassall (1999) found, for instance, that northern grasshoppers hatch larger and grow faster than their southern conspecifics. However, the shorter nymphal development periods result in relatively smaller adults than in more southern, warmer, sunnier localities. Berner and Blankenhorn (2006) found higher body mass, longer development time and constant growth rate in populations from lower altitudes, but within a population heavier individuals had higher growth rates.

We found no evidence for the predicted interaction effect between population origin and breeding temperature. Several issues need to be addressed here to interpret this result. In northwestern Europe, most grasshopper species are high temperature specialists (Willott and Hassall 1998). They do not show bell-shaped reaction norms for life history traits relative to ambient temperature with a declining profile at high temperatures like in many ectothermous species; they typically show increasing performance for many life history traits with temperature reaching a plateau as high as 45°C (Walters and Hassall 2006). Higher temperatures are lethal. So, maximal performance is very close to the lethal level making thermoregulation of key significance to survival. Consequently, this type of reaction norm does not leave much scope for further directional selection towards higher optimal body temperatures. Moreover, the efficient thermoregulatory behavior in grasshoppers, and in *C. brunneus* in particular (e.g., Willott 1997; Willott and Hassall 1998), allows coping with thermal environmental constraints in a flexible way. This may lead to evolutionary stasis (Huey et al. 2003). Moreover, the thermal differences between urban and rural landscapes are the highest during the night and during winter (Souch and Grimmond 2006) when grasshoppers are not active. Hence, the difference in thermal profile experienced by urban and rural grasshoppers in the field may be of minor significance relative to their behavioral thermoregulation capacities. This does not necessarily exclude differences in microhabitat use for thermoregulation between both landscape types. The high incidence of concrete substrates in the urban environment may facilitate reaching high body temperatures. This aspect needs further comparative behavioral study in the field.

Besides the direct behavioral impact, urban climates may also affect growing conditions. Milder winter conditions and nights are probably associated with a longer growing season (and longer activity periods) resulting in different time constraints between urban and rural populations that are similar to the differences observed along altitudinal and latitudinal gradients. Telfer and Hassall (1999) did not find latitudinal differences for body mass of *C. brunneus* in England, but they observed a positive correlation between female body mass at eclosion and minimum January temperature. This matches with our observations in urban and rural populations. Telfer and Hassall (1999) found smaller eggs under warmer conditions, whereas we found heavier eggs in urban populations compared to rural ones. But what they found is a negative relationship between egg size and summer temperature that are not so different between urban and rural landscapes. Heavier eggs in urban populations may simply result from an allometric effect of much heavier females in those areas compared to rural areas.

The pattern of heavier females in populations living under warmer climatic conditions appears to be general for Acrididae species. Hence, we may predict similar life history effects as shown here for other grasshopper species. The contrast between urban and rural climate is more pronounced to the north (Wienert and Kuttler 2005). Hence, ecotypic differentiation for climate-related life history traits along a urbanization gradient is predicted to be larger in northern regions. On the other hand, it is less straightforward to make generalizations about movement-related morphology for other grasshopper species as functional connectivity of the same landscape may vary among different species (Baguette and Van Dyck 2007).

In summary, several studies have shown that urbanization impacts on species richness and community composition for several taxonomic groups (McKinney 2002), but here we have shown evidence for ecotypic differentiation in movement-related morphology and climate-related life history traits at the intra-specific level between urban and rural grasshopper populations.

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