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From multifamily residences to studio apartments: shifts in burrow structures of European rabbits along a rural-to-urban gradient

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Abstract

European rabbits (*Oryctolagus cuniculus*) are currently declining in most rural areas throughout central Europe, while city populations often reach high densities. We asked whether and how altered environmental conditions affect the social organization and burrow structures of European rabbit populations located at urban, suburban and rural sites in and around Frankfurt a.M. in Germany. Burrow densities (numbers per ha) increased along the rural-to-urban gradient, accompanied by a gradual shift from accumulated towards more evenly distributed burrows. Burrows became smaller and less complex with increasing degree of urbanity, and accordingly, also the number of rabbits inhabiting the same burrow decreased. It remains unclear whether urbanization first led to smaller rabbit group sizes and burrow structures then shifted as a consequence of this, or vice versa. Nevertheless, for both scenarios, we propose that increased structural heterogeneity of urban landscapes is the major factor behind the observed effects, as mosaic-like habitat patches in cities provide high and steady resource availability compared with the agriculturally transformed, open landscapes characterizing most rural areas in central Europe.

Introduction

Several small- to medium-sized mammals in Western Europe colonize urban regions, partly due to the destruction of their original habitats, or because urban regions offer a new set of alternative habitats (McKinney, 2002; Ditchkoff, Saalfeld & Gibson, 2006; Baker & Harris, 2007). The spread of introduced diseases such as myxomatosis since the 1950s (e.g. in Great Britain: Armour & Thompson, 1955), and rabbit haemorrhagic disease in the late 1980s (e.g. in Spain: Villafuerte *et al*., 1995), in combination with intensified agricultural practices, altered forms of land use (Moreno & Villafuerte, 1995; Delibes-Mateos *et al*., 2010), and hunting (Angulo & Villafuerte, 2004) have driven several rural populations of European rabbits (*Oryctolagus cuniculus*, L. 1758) close to extinction (Lees & Bell, 2008; Ferreira *et al*., 2014). The species is currently categorized as 'nearly-threatened' by the IUCN (2014) in its original distribution area on the Iberian Peninsula. In contrast, rabbit populations in several German cities appear to be largely unaffected by this steep decline and reach highest densities (Arnold *et al*., 2013; Ziege *et al*., 2013), characterizing the European rabbit as an 'urban adapter' or even as an 'urban exploiter' (McKinney, 2002, 2006). Hence, studying the characteristics of urban ecosystems and their effects on the ecology and behaviour of urban wildlife (urban ecology) becomes less of an anthropocentric question, but more of a practical issue for conservation management (Shochat *et al*., 2006; Alberti *et al*., 2008).

Urbanization creates highly structured landscapes characterized by spatial heterogeneity of ecological conditions and habitat fragmentation by structures that constrain dispersal (Baker & Harris, 2007; McKinney, 2008; Kowarik, 2011). Accordingly, most research on urban wildlife populations has focused on how landscape structures affect movement patterns and demonstrated that habitat fragmentation and heterogeneity leads to smaller individual home ranges in red fox (*Vulpes vulpes*: Adkins & Stott, 1998) and badgers (*Meles meles*: Davison *et al*., 2009). The influence of urban landscape features on behaviours related to nesting, denning and burrowing, however, remains largely unknown. Empirical data on those aspects are a prerequisite for predicting and managing human–wildlife conflicts, for example, when mammals show a predilection to establish burrows or dens in gardens, or in the proximity of buildings or roads (for European badger in the UK, see Davison *et al*., 2008).

To date, only a single study has examined the effects of urbanization on burrow structures in a mammalian species. Davison *et al*. (2008) found main burrows of urban badger populations in southern England to have significantly fewer entrance holes compared with those located in rural areas. The authors discuss three not mutually exclusive hypotheses to explain those patterns: First, burrows with fewer entrance holes could simply reflect a more recent migration – assuming that the complexity of burrow systems increases over time (Roper, 1992). Second, limitations in available space for burrowing could explain this pattern. Third, potential shifts in social organization of urban badger populations could be reflected by smaller group sizes, which, in turn, ought to result in smaller burrows with fewer entrances. Indeed, group size and structure of rabbits depend on several ecological factors that are known to vary along the rural-to-urban gradient, such as habitat quality (vegetation cover, soil conditions), population density and especially predation risk (reviewed in Lees & Bell, 2008).

For small- to medium-sized mammals, burrows often function as refuge from predation. Not only the intensity of predation affects the construction of burrows through changes in group size and composition (Villafuerte & Moreno, 1997), but prey species can alter the burrowing behaviour directly in response to increasing predation risk (Harper & Batzli, 1996). The authors showed that burrows of voles (*Microtus* sp.) had fewer entrances and fewer short, blind escape tunnels in pens with no predation risk (but no changes reported by M. Liesenjohann, A. Barber & J. A. Eccard, pers. comm.). Studies on predation pressure along the rural-to-urban gradient yielded conflicting results ('predation paradox': Shochat, 2004; Fischer *et al.*, 2012), making it difficult to derive specific predictions on burrow structures of urban rabbits. Some studies reported on reduced predation rates and lower vigilances of prey species (Gering & Blair, 1999; Møller, 2008), while others found higher densities of predators in urban environments (e.g. racoons, *Procyon lotor*: Prange, Gehrt & Wiggers, 2003) and higher predation rates (e.g. nests of Japanese quail, *Coturnix coturnix japonicus*: Jokimäki & Huhta, 2000).

In the present study, we compared burrow structures of several populations of European rabbits from urban, suburban and rural sites in and around Frankfurt a.M., Germany. Rabbit populations have been established for several decades in the city district of Frankfurt (at least since 1930; Stadtarchiv Frankfurt), and so potential differences in size and complexity of burrow structures are unlikely to reflect different time spans of burrow establishment (*sensu* Davison *et al.*, 2008). In addition to increasing population densities along the rural-to-urban gradient (Ziege *et al.*, 2013), limitation of suitable sites for burrow construction could result in larger social groups inhabiting multi-entrance burrows. Vegetation cover typically decreases towards the city centre (Shochat *et al.*, 2006; McKinney, 2008); however, sites with shrub cover are preferred for burrowing (Palomares, 2003; Gea-Izquierdo, Muñoz-Igualada & San Miguel-Ayanz, 2005), and rabbits are known to form larger and more cohesive groups when such sites are rare (Bell, 1983; Cowan, 1987). A conflicting prediction would be that more complex urban landscape structures result in an increased availability of suitable sites for burrow construction, and also reduced predation risk may be reflected by smaller rabbit groups, pairs, or even single individuals that might use smaller burrows with fewer entrance holes. We tested these contrasting predictions by comparing several parameters related to burrow structure and complexity between different sites in and around Frankfurt. Unlike previous studies that relied on pairwise comparisons of urban versus non-urban sites (e.g. Davison *et al.*, 2008), we established a continuous variable, the 'degree of urbanity', as a quantitative measure of anthropogenic impact for each study site (Ziege *et al.*, 2013). This incorporated several variables related to the degree of disturbance by residents and anthropogenic landscape alterations.

Material and methods

Study sites and degree of urbanity

The impact of human activities typically decreases from the centre towards the less densely populated periphery of a city (Adams, 1994). We chose our study sites to reflect this urban-to-rural gradient and included nine parks in the city centre of Frankfurt (former rampart areas), four parks located at the former periphery of the administrative district in Frankfurt and three adjacent rural areas (Table 1, Supporting Information Fig. S1). Alberti, Botsford & Cohen (2001) noted that the degree of urbanity does not necessarily decrease continuously towards the outskirts of a city (see also McKinney, 2008). We, therefore, refrained from categorizing our study sites into distinct classes of urbanity, but calculated a continuous variable for each of our 16 study sites (Ziege *et al.*, 2013). To this end, we established the following variables (Table 2):

(1) Numbers of residents located within a radius of 500 m were obtained from the registration office (Einwohnermeldeamt) of Frankfurt a.M. (updated: 31 October 2010). (2) The intensity of disturbance by humans (pedestrians and bikers) and leashed or unleashed dogs was recorded during the main activity period of the rabbits at dawn and dusk. Counting points were randomly selected within each study site using the ArcMap Random Point Generator. The appropriate number of transect belts within study sites was determined in relation to the size of the area. These random points were used as starting points to draw a virtual transect line of 25 m length, orientated to the North. During each count, all pedestrians, bikers and dogs crossing this transect line were counted for three minutes; measurements were repeated after 30 min. In total, 20 counts per site were performed on five consecutive days (Wednesday–Sunday) in July and August 2011. In order to obtain comparable data, we measured one rural, one suburban and one urban park simultaneously.

(3) The proportion of artificial ground cover (e.g. streets, play grounds) within the study areas was determined using ArcGIS 10 and map material provided by the land surveying office (Stadtvermessungsamt) of the city of Frankfurt. We log-transformed the data and subjected the variables to a principal component analysis. One principal component

Table 1 Location, size, 'degree of urbanity' (principal component, see main text) and burrow density of 16 study sites situated along the rural-to-urban gradient in and around Frankfurt a.M.

Study sites	Coordinates		Size (ha)	Degree of urbanity	Burrow density (number/ha)
Rural					
Bad Vilbel	N 50°9.418	E 8°42.820	49.00	−2.03	0.25
Kriftel	N 50°4.504	E 8°27.886	49.00	−1.87	0.25
Maintal	N 50°8.653	E 8°49.094	49.00	−1.70	0.30
Suburban					
Ostpark	N 50°7.251	E 8°43.364	30.20	−0.25	1.82
Rebstockpark	N 50°6.674	E 8°36.773	21.10	−0.21	1.19
Grüneburgpark	N 50°7.647	E 8°39.608	27.00	−0.17	0.11
Miquelanlage	N 50°7.970	E 8°39.524	5.50	0.08	2.55
Urban					
Site 1	N 50°6.723	E 8°40.220	3.64	0.45	4.67
Site 2	N 50°6.999	E 8°41.503	4.90	0.56	2.24
Site 3	N 50°7.098	E 8°40.946	3.37	0.65	2.67
Site 4	N 50°7.001	E 8°40.529	3.66	0.67	0.82
Site 5	N 50°6.606	E 8°40.323	1.00	0.69	3.00
Site 6	N 50°6.673	E 8°41.608	3.53	0.71	2.83
Site 7	N 50°6.865	E 8°40.263	1.33	0.73	4.51
Site 8	N 50°7.160	E 8°41.198	2.18	0.74	4.59
Site 9	N 50°6.870	E 8°41.650	1.50	0.97	3.33

Table 2 Mean ± SD of variables that were used to calculate the 'degree of urbanity' of the three rural, four suburban and nine urban study sites

	Rural	Suburban	Urban
Number of residents located within a radius of 500 m	40.17 ± 29.52	466.48 ± 194.15	5395.72 ± 3970.18
Intensity of disturbances induced by humans and leashed/unleashed dogs $\text{min}^{-1}\ \text{ha}^{-1}$	0.01 ± 0.00	0.14 ± 0.10	1.68 ± 0.74
Proportion of artificial ground cover in % of the total study area	0.06 ± 0.00	13.32 ± 3.50	17.11 ± 3.63

(henceforth referred to as the 'degree of urbanity') with an Eigenvalue >1 was retrieved that explained 92.30% of the variance.

Burrow densities and distribution patterns

In October 2011, two persons walked transects approximately 5 m apart and located a total of 191 burrows. Burrow locations (GPS coordinates) were determined using a Garmin 12 GPS and processed using Arcview GIS 3.3 (ESRI, Redlands, CA, USA). We expressed densities as numbers of burrows per ha and tested for a correlation between the 'degree of urbanity' (see above) and burrow densities by means of a non-parametric Spearman rank correlation.

We tested whether suitable sites for burrow construction are limited in urban areas, in which case burrows ought to be less uniformly distributed than in rural areas. Burrow distribution patterns were assessed using two different approaches: The first was adopted from Lombardi *et al.*, 2003 who studied rabbit burrow distributions in three different landscapes (ecotone, grassland and scrubland) by dividing a given study area into 50 × 50 m quadrants. The mean number of burrows in quadrants $(\bar{x})$ was determined and the index of dispersion I_D calculated (Krebs, 1999):

$$I_D = \frac{\textit{observed variance } s^2}{\textit{observed mean } \bar{x}}$$

I_D values close to 0 indicate a uniform distribution, whereas values much larger than 1 indicate an aggregated distribution pattern. I_D is approximately distributed as χ^2 with n-1 degrees of freedom (v) whereby n is the number of quadrants: $\chi^2 = I_D (n-1)$. Z-values were calculated as follows (Krebs, 1999):

$$Z = \sqrt{2\chi^2} - \sqrt{(2v-1)}.$$

At $\alpha = 0.05$, the spatial distribution would be random if $1.96 \geq Z \geq -1.96$, while $Z > 1.96$ or $Z < -1.96$ indicate aggregated or uniform distributions, respectively (Krebs, 1999). The second approach refrains from assigning burrows to distinct quadrants within the study area but considers the distances between each burrow and its nearest neighbour based on GPS locations (see Gea-Izquierdo *et al.*, 2005). We used the Donnelly modification of the Clark and Evans test and calculated the index of aggregation R_D to determine whether the observed burrow distribution patterns deviate from random patterns (Krebs, 1999). R_D values approach 0 if spatial pattern is aggregated and thus, Z-values < −1.96 indicate an aggregated spatial distribution (Krebs, 1999).

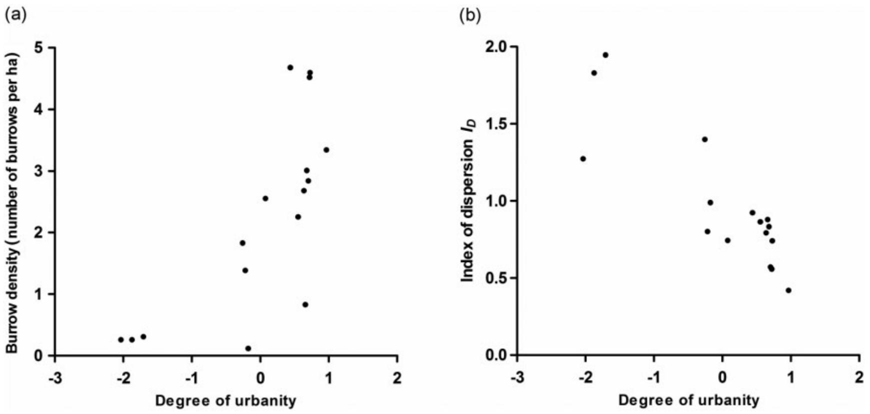

Figure 1 Correlation between the 'degree of urbanity' and (a) numbers of rabbit burrows per ha and (b) the index of dispersion (I_D).

We correlated I_D and R_D values with the 'degree of urbanity' using a Spearman rank correlation.

Group size

To establish whether urbanization affects burrow complexity indirectly through shifts in rabbit group sizes, we used domestic ferrets (*Mustelo putorius furo*) to chase rabbits out of their burrows. This was done as part of a regular hunting scheme, organized by the city of Frankfurt and conducted by local hunters (hunting licence ID 1000250221). This approach allowed us to determine rabbit group sizes of 41 burrows in the city centre, 14 at suburban study sites and four in rural areas. Due to financial constraints and hunting law regulations, we could not use this approach for all study sites. However, for additional 10 burrows (five rural and five suburban) behavioural observations provided information on group sizes. We observed those burrows from a distance of 50 m on three consecutive days during dusk and dawn in October 2011 and noted the maximum number of rabbits leaving the same burrow system. A Spearman rank correlation was used to test for an effect of the 'degree of urbanity' on group sizes.

Our experiments comply with the current laws and ethical standards of Germany (project listed at the animal welfare commission for the State of Hesse under ID: V54-19c 20/15 – F 104/59).

Complexity of burrow structure

We determined numbers of burrow entrances for 132 burrows as an estimate of burrow size. An additional 31 burrows were identified but access was restricted since they were located on private ground or covered by impenetrable vegetation, and entrances of another 28 burrows were partly destroyed by human activities. A Spearman rank correlation was used to test for an effect of the 'degree of urbanity' on the numbers of entrances per burrow. We also tested if numbers of burrow entrances correspond with the number of rabbits that inhabit that burrow (see above) using a Spearman rank correlation.

Moreover, we randomly selected 61 burrows (19 rural, 23 suburban and 19 urban) for an in-depth analysis of external burrow structures (Kolb, 1985). We measured distances between each burrow entrance and at least two others by using a range finder and handheld telescope poles. This approach allowed us to draw a sketch map (1:100) of each burrow and to determine mean distances between all entrances. For each entrance, we measured the height and width of entrance and inlet. The entrance was defined as the area of the main hole leading into soil, whereas the inlet was the area of the funnel in front of the hole shaped by rabbits while entering and leaving the burrow.

We log-transformed all structure-related variables (number of burrow entrances, mean distance between entrances, mean width/height of burrow entrances and inlets) and subjected them to principal component analysis. One principal component (PC) with an Eigenvalue >1 was retrieved that explained a total of 56.64% of the variance. A Spearman rank correlation was used to test for a correlation between this burrow structure-related PC and the 'degree of urbanity'.

We calculated multiple correlations, often using the same variables (like the 'degree of urbanity'). However, even the most conservative correction of significance levels to avoid alpha-error inflation [i.e. Bonferroni correction: $\alpha = 0.05/$ number of multiple comparisons $(0.05/6) = 0.008$] would not affect our conclusions (all correlations $P \leq 0.003$).

Results

We found numbers of rabbit burrows per ha to increase with increasing 'degree of urbanity' (Spearman's $r = 0.77$, $P < 0.001$, $n = 16$; Fig. 1a). When considering the distribution pattern of burrows we found a significant deviation from a random distribution for all three rural study sites, where burrows were aggregated (I_D: Z-values between 2.40 and 7.40, R_D: Z-values between –3.15 and –1.97). This was also the case for one suburban site (Ostpark, I_D: Z-value = 3.05, R_D: Z-value = –3.847), while burrow distribution in all other suburban and almost all urban areas was not significantly different from a random distribution (suburban sites excluding Ostpark: Z-values for I_D between –1.21 and –0.09, for R_D

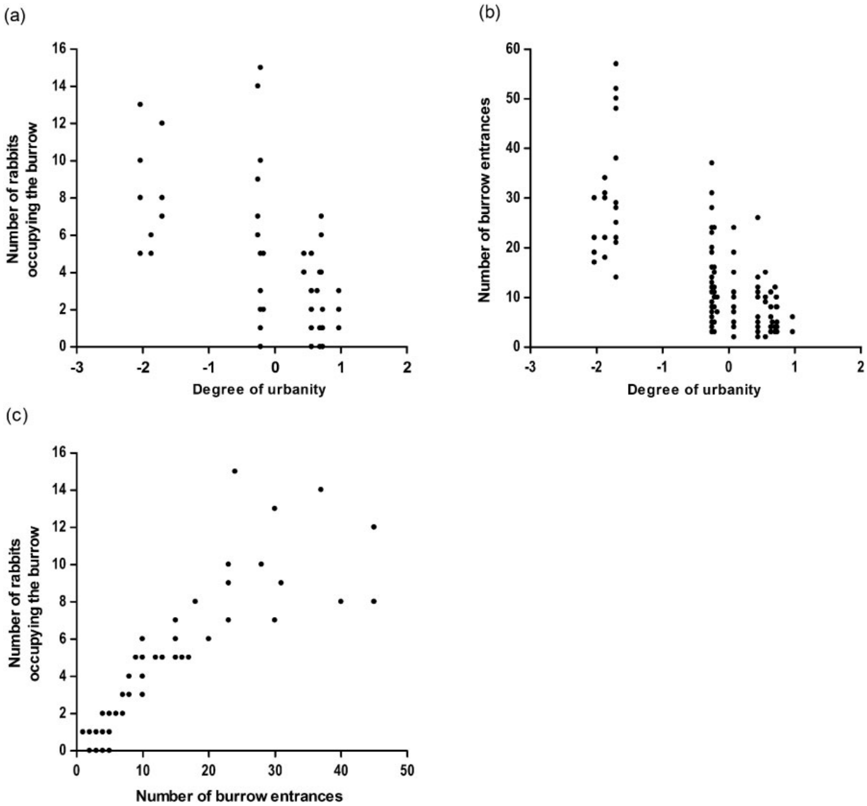

Figure 2 Correlation between the 'degree of urbanity' and (a) numbers of rabbits inhabiting a burrow and (b) numbers of burrow entrances. (c) Correlation between numbers of burrow entrances and numbers of rabbits inhabiting the same burrow system.

between –1.57 and 1.26; urban sites: Z-values for I_D between –1.13 and –0.13, Z-values for R_D between –0.67 and 1.87). In case of the urban study sites number 3 and 7 (see Table 1) calculated Z-values for R_D were > 2.03 and thus, suggesting a uniform distribution pattern. Spearman rank correlations for both indices confirmed a significant gradual shift from an aggregated towards a random to uniform distribution pattern along the rural-to-urban gradient (I_D: $r = -0.85$, $P < 0.001$, $n = 16$, Fig. 1b; R_D: $r = 0.70$, $P = 0.003$, $n = 16$, Supporting Information Fig. S2).

Group sizes decreased significantly along the rural-to-urban gradient ($r = -0.61$, $P < 0.001$, $n = 69$; Fig. 2a). Moreover, the number of burrow entrances decreased as a function of the 'degree of urbanity' ($r = -0.59$, $P < 0.001$, $n = 132$; Fig. 2b). Accordingly, the number of burrow entrances correlated positively with the number of inhabiting rabbits ($r = 0.93$, $P < 0.001$, $n = 69$; Fig. 2c).

Another Spearman rank correlation revealed a negative correlation between the burrow structure-related PC and the 'degree of urbanity' ($r = -0.63$, $P < 0.001$, $n = 61$; Table 3, Fig. 3). Specifically, numbers of burrow entrances as well as distances between burrow entrances decreased continuously along the rural-to-urban gradient (Table 4). This trend was also found for the height of burrow entrances and their inlets. The mean width of burrow entrances was comparable for burrows situated in rural and suburban areas, but was significantly narrower for burrows at urban sites. By contrast, the mean width of the burrow inlet reached greatest values for burrows at suburban sites but was similar for burrow systems located in urban and rural areas (Table 4).

Table 3 Axis loadings for the burrow structure-related principal component of $n = 61$ burrows

Structure-related variables	Axis loading
Number of entrances	0.72
Distance between entrances	0.83
Entrance width	0.79
Entrance height	0.80
Inlet width	0.58
Inlet height	0.77

Discussion

The proportion of sealed soil surface increases along the rural-to-urban gradient (Shochat *et al.*, 2006; McKinney, 2008; Table 2), and reduced availability of sites that are suitable for burrow construction could lead to fewer but larger burrow systems hosting larger groups (first hypothesis). However, our results revealed a very different pattern: burrow densities increased with increasing urbanity, which was accompanied by a shift from highly accumulated towards more evenly distributed burrows. Moreover, burrow systems became gradually smaller and less complex, and group sizes (i.e. numbers of

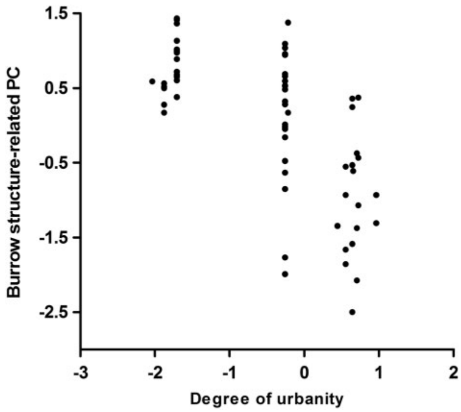

Figure 3 Correlation between the 'degree of urbanity' and the burrow structure-related PC (for details, see main text).

Table 4 Mean ± SE for burrow structure-related variables of 19 rural, 23 suburban and 19 urban burrow systems

	Rural	Suburban	Urban
Number of entrances	31.9 ± 2.2	17.0 ± 2.0	7.1 ± 2.2
Distance between entrances (m)	7.4 ± 0.5	5.3 ± 0.5	3.2 ± 0.5
Entrance width (cm)	18.5 ± 0.6	18.4 ± 0.6	16.0 ± 0.6
Entrance height (cm)	20.3 ± 0.6	17.4 ± 0.6	15.3 ± 0.6
Inlet width (cm)	45.6 ± 2.2	54.8 ± 2.0	41.3 ± 2.2
Inlet height (cm)	93.4 ± 4.6	74.3 ± 4.2	62.0 ± 4.6

rabbits occupying the same burrow system) decreased along the rural-to-urban gradient. Thus, our results support the second (alternative) hypothesis, which assumed that urban rabbit populations could benefit from increased structural heterogeneity of urban landscapes.

Shifts in burrow densities and distribution patterns

Higher burrow densities in urban compared to rural populations and shifts in distribution patterns from highly accumulated towards randomly/uniformly distributed suggest that urban habitats provide more opportunities for rabbits to establish burrow systems (for comparison, see also Lombardi *et al.*, 2003). Areas in modern cities without buildings, or streets, like parks and gardens, are often structurally highly diverse and provide a variety of ecological niches (McKinney, 2008; Kowarik, 2011). European rabbits are known to reach high densities in rural areas where availability of cover (including suitable ground for burrow construction) and access to food are high, that is, landscapes with high land-use diversity (Lombardi *et al.*, 2003; Calvete *et al.*, 2004; Guerrero-Casado *et al.*, 2013). Shochat *et al.* (2006) described cities as a mosaic of different land-use forms with habitat management strategies rendering resources more continuously available that are otherwise highly variable in temporal and spatial dimensions. By contrast, rural, agriculturally transformed areas are nowadays often characterized by open, homogenous landscapes in which vegetation cover is scarce.

Decreasing burrow size and complexity

Artificial structures could hinder the expansion of individual burrows, leading to smaller burrows at urban sites. Moreover, at sites where rabbits established burrows close to roads, buildings or private gardens, we found several such burrows to be destroyed (and thus, abandoned) by private land owners or as part of urban management strategies (see also Davison *et al.*, 2008 for urban badger populations in the UK). However, it seems unlikely that destruction of burrows plays a major role, as several burrows at urban sites were well protected from direct human impact. Another possibility would be that soil conditions affected the complexity of burrow systems; for example, rabbit burrows are reported to be smaller in loose, sandy soils (Cowan, 1987; Gea-Izquierdo *et al.*, 2005). In this study, we refrained from performing detailed analyses of soil compositions but restricted data collection to qualitative observations because at all study sites at least one small ('simple') burrow and one complex burrow system with several entrances was found. Obviously, soils along the rural-to-urban gradient considered in this study support the creation of complex burrow systems and are neither too loose (i.e. sandy) such that entrances would spontaneously collapse, nor too hard for burrowing.

Why then do urban rabbits form smaller, less complex burrows inhabited by fewer individuals compared to rural populations? First, in large groups, the per capita energy loss during cold periods is smaller (sugar glider, *Petaurus breviceps*: Fleming, 1980; alpine marmots, *Marmota marmota*: Arnold, 1988). Second, large burrows with many entrances provide better protection from predators (rabbits: Cowan, 1984; voles: Harper & Batzli, 1996). Urban populations may benefit less from establishing large burrows because ambient temperatures tend to be higher (Pickett *et al.*, 2001), while predation pressure may decrease (see Introduction). Based on qualitative observations in our study area, we doubt that predation risk alone explains altered burrow structures and that predation risk decreases continuously along the rural-to-urban gradient in a way that would satisfactorily explain the observed gradual change of burrow structures. We further suggest that shifts in the height and width of burrow entrances could be related to differences in utilization frequencies and thus, intensity of soil erosion. For instance, as an expression of reduced anti-predator behaviour in urban and suburban rabbit populations (fewer) rabbits may enter and leave their burrows less often and at a reduced speed compared with rural rabbits (see also Ziege *et al.*, 2013). Finally, rabbits are known to form large social groups when resources are limited (reviewed in Lees & Bell, 2008), but neither food nor sites for burrow construction seem to be currently limited in German cities (Arnold *et al.*, 2013; Ziege *et al.*, 2013).

In our study, we provide insights into changes in social organization and burrow structure in a species that is currently declining in most rural areas of Europe (reviewed in Lees & Bell, 2008). As suggested for rabbit populations within their natural distribution range on the Iberian Peninsula (Ferreira *et al*., 2014), we also provided evidence that habitat management is a key factor for the preservation of stable German rabbit populations. This is a first case study, and the rural-to-urban gradients detected here may be the results of specific characteristics of the landscape structure, landscape management practices or ecology of Frankfurt a.M. Nevertheless, our present study can serve as a starting point for future investigations from which we hope to gain more insights into the ecology and behaviour of rabbit populations experiencing different degrees of urbanization. They will be of immediate help for conservation (city) planers and will allow discussing our present results within a broader framework.

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Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Fig. S1. Study sites within (a) the rural area *Kriftel*, (b) the suburban *Rebstockpark* and (c) the inner city centre of Frankfurt a.M. (urban site number 1, 5 and 7 in Table 1). White rectangles indicate rabbit burrows. Source: Google Earth.
Fig. S2. Correlation between the 'degree of urbanity' and the Donnelly index of aggregation (R_D).