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Extended diurnal activity patterns of European rabbits along a rural-to-urban gradient

Madlen Ziege^{a,*}, Denise Babitsch^a, Mareike Brix^a, Stefanie Kriesten^a,
Susanne Straskraba^a, Sandra Wenninger^a, Torsten Wronski^b, Martin Plath^c

^a Department of Ecology & Evolution, Goethe University Frankfurt, Max-von-Laue-Str. 13, D-60438 Frankfurt am Main, Germany

^b Bristol Zoological Society, Conservation Science, Clifton, Bristol, BS8 3HA, UK

^c College of Animal Science and Technology, Northwest A&F University, Yangling, Shaanxi 712100, China

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ABSTRACT

Effects of urbanization on the population dynamics of wildlife species range from entirely negative (leading to local population extirpation) to positive effects. Relaxed predation on species like European rabbits (*Oryctolagus cuniculus*) in cities not only lowers extrinsic mortality rates, but could also facilitate advantageous behavioral modifications, as less time needs to be invested in anti-predator behaviors. We studied diurnal activity patterns of rabbits along a rural-to-urban gradient in and around Frankfurt am Main (Germany), where population densities increase from the periphery towards the city center. Compared to individuals from rural sites, rabbits from urban and suburban sites spent, on average, more time outside their burrows, invested less time in anti-predator behavior, and showed reduced rhythmicity in daytime activity patterns, including a weaker midday resting phase. Anthropogenic disturbance was considerably higher at urban and suburban sites compared to rural ones; still, rabbit behavior was less affected by anthropogenic disturbance. This was confirmed experimentally by chasing the members of different social groups into their burrows: while rabbits at rural and suburban sites uniformly fled into their burrows, this was not the case in 93% of urban rabbit groups. Also, times until individuals reappeared above ground decreased when we repeated this measurement on several subsequent days. Our study provides further evidence that not only direct effects (like landscape alterations and altered resource availability), but also indirect effects (here: behavioral changes following altered predation regimes and subsequent habituation to other sources of disturbance) need to be considered when formulating predictions about how urbanization affects wildlife populations.

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Introduction

With an ever increasing human world population (Kremer, 1993), urban regions are rapidly expanding (UNPD, 2014), causing landscape modifications that have significant consequences for wildlife species (Ditchkoff et al., 2006; Magle and Angeloni, 2011; reviewed in Ryan and Partan, 2014). Urbanization creates mosaic-like heterogeneous habitat structures, and urban management strategies increase the availability of some resources (like food or suitable sites for burrow construction or nesting), but at the same time lead to the decrease of others, e.g. habitat fragmentation constrains movement and dispersal (Shochat et al., 2006; Pickett et al., 2008; Evans et al., 2009; reviewed in Rodewald and

Gehrt, 2014). Hence, urbanization has opposing effects on different wildlife taxa, ranging from population declines or local population extirpation in some species (Iossa et al., 2010) to increased population recruitment in so-called ‘urban exploiters’ (e.g., fox squirrels, *Sciurus niger*: McCleery et al., 2008; European badgers, *Meles meles*: Harris et al., 2010; European rabbits, *Oryctolagus cuniculus*: Ziege et al., 2015, 2016 or birds: Møller et al., 2012). Consequently, urban regions may become increasingly important from a conservation-oriented perspective, especially for species that are declining in rural areas but thrive in urban habitats (McKinney, 2008; Ramalho and Hobbs, 2012).

Moreover, alterations in predator-prey interactions and increased anthropogenic nuisance need to be considered when formulating predictions about how wild animals’ life histories and behavior in urban and suburban populations might differ from those of their rural counterparts (Shochat et al., 2006; Rodewald and Gehrt, 2014). Some studies reported on declining

* Corresponding author.

E-mail address: madlen.ziege@mailbox.org (M. Ziege).

Table 1

Detailed information for the six study sites situated along a rural-to-urban gradient in and around Frankfurt a.M., Germany. The ‘degree of urbanity’ reflects principal component values as described in Ziege et al. (2013, 2015, 2016) to characterize sites according to several ecological variables related to anthropogenic landscape alteration and human nuisance.

Study sites	Coordinates		Rabbit density (individuals/ha)	Degree of urbanity
Rural				
Bad Vilbel	N 50° 9.418	E 8° 42.820	0.88	−1.00
Maintal	N 50° 8.653	E 8° 49.094	3.38	−0.96
Suburban				
Rebstockpark	N 50° 6.674	E 8° 36.773	15.02	−0.28
Ostpark	N 50° 7.251	E 8° 43.364	19.14	−0.16
Urban				
Site 1	N 50° 6.999	E 8° 41.503	9.07	0.97
Site 2	N 50° 7.160	E 8° 41.198	13.95	1.42

predator densities and lower vigilance of prey species in urban environments (birds: Møller, 2008; fox squirrels: McCleery et al., 2008), while others found higher densities of certain predators (cats, *Felis catus*: Baker et al., 2008; Cooper’s hawk, *Accipiter cooperii*: Rosenfield et al., 1995 or racoons, *Procyon lotor*: Prange et al., 2003; see also “predation paradox”: Shochat et al., 2006). In some cases, reduced predation may act together with increased structural heterogeneity and resource availability to facilitate high population densities in cities. However, secondary (e.g., behavioral) consequences of reduced predation and increased resource availability are little investigated and so their impact on population ecology is little understood (Lehrer et al., 2011).

In recent decades populations of European rabbits are declining in most rural landscapes throughout central and southern Europe (Virgós et al., 2003; Moreno et al., 2008; Arnold et al., 2013; Ferreira et al., 2014) and the species is currently classified as “Near Threatened” by the IUCN Red List (Smith and Boyer, 2008). A case study on German European rabbit populations reported rural landscapes to become increasingly “sterile”, leading to a loss of habitat for this species (Ziege et al., 2013, 2015, 2016). By contrast, high urban habitat heterogeneity led to flourishing rabbit populations, which can become a nuisance to German city administrators and private land owners (Arnold et al., 2013; Ziege et al., 2013, 2015). Most likely, the trend of flourishing rabbit populations in cities is further brought about by relaxed predation (Ziege et al., 2015, 2016). Although common natural predators such as red foxes, *Vulpes vulpes* (Gloor et al., 2001), mustelids like *Martes foina* and *Mustela erminea* (Duduš et al., 2014) or birds of prey like kestrels, *Falco tinnunculus* (Kübler et al., 2005), northern goshawks, *Accipiter gentilis* (Rutz, 2006) or sparrowhawks, *Accipiter nisus* (Risch et al., 1996) can also reach high densities in cities, their mere presence does not necessarily mean that they also exert strong predation on urban rabbit populations (see above for the “predation paradox”). For example, as reported for red foxes (Contesse et al., 2004) or Cooper’s hawk (Estes and Mannan, 2003), predators in cities sometimes start using other (more abundant) food sources. Moreover, both, predator and prey species can alter their activity patterns in habituation to the permanent anthropogenic disturbance in modern cities which, in turn, can lead to changes in natural predation regimes (Riley et al., 2003; Ditchkoff et al., 2006).

Urban areas can only provide suitable habitats when wild animals are able to cope with the permanent human presence and proximity (Partecke et al., 2006; Evans et al., 2010; Ryan and Partan, 2014). Thus, it is not surprising that many studies reported significantly shorter flight initiation distances (birds: Møller, 2008; mammals: McCleery, 2009; Ziege et al., 2013; Bateman and Fleming, 2014; reviewed in Ryan and Partan, 2014) or a reduction in time spent on anti-predator behaviors (squirrels: McCleery, 2009; Chapman et al., 2012). These behavioral modifications allow for coexistence with humans without behavioral disruption, leading to lower energy expenditure and reduced stress responses (e.g.,

Ditchkoff et al., 2006; French et al., 2008; Møller, 2012; but see Frid and Dill, 2002 and Lehrer et al., 2011 for conflicting results, supporting the “risk-disturbance hypothesis”).

Several studies demonstrated the ability of the European rabbit to adapt behaviorally to different habitat types characterized by different predation risk and availability of resources like refuge and food (Lombardi et al., 2003, 2007). However, those studies only considered rural rabbit population, while comparisons of populations exposed to different levels of urbanization are as yet lacking. We argue that, overall, behavioral changes due to an altered predation regime would present yet another aspect to consider when explaining the strong population increase of urban rabbit populations in Central Europe (see also Lombardi et al., 2003, 2007 for rural rabbit populations). Following investigations on burrow distributions and latrine marking behavior of European rabbit populations in and around Frankfurt a.M. (Ziege et al., 2015, 2016), the aim of this study was to add knowledge to the question of whether this mammal shows advantageous behavioral alterations (e.g., extended activity patterns, reduced vigilance behavior and more social interactions) in response to a human-modified environment. This question is also of interest for the future conservation and management of this once common mammalian species in Europe.

We predicted (1) that urban and suburban rabbits, due to relaxed predation pressure, spend more time outside their protective burrow than rural rabbit populations. We further predicted (2) that urban and suburban rabbits should show less anti-predator behavior when outside their burrow than their rural conspecifics. Based on the study of Adams et al. (1987) who found rural black-tailed prairie dogs (*Cynomys ludovicianus*) to conceal themselves considerably longer in their burrows after a simulated predator attack (in the form of a human approach) compared to their urban conspecifics, we further predicted (3) that urban and suburban rabbit populations recover faster from such a human-induced, simulated predator attack, too (i.e. spend less time in their burrows). Finally, we predicted (4) that urban and suburban rabbit population habituate faster to disturbance by repeated human approaches compared to their rural conspecifics.

Material and methods

Ethics statement

For our present study, no animals were killed or manipulated, i.e., data collection was non-invasive. Our study on the behavioral ecology of European rabbits was approved by the animal welfare commission of the State of Hesse (ID: V54-19c 20/15-F 104/59).

Study sites

We chose our study sites to reflect a rural-to-urban gradient in and around Frankfurt a.M. in Germany and thus, observed rab-



Fig. 1. Study sites.

(a) One of our rural study sites at Maintal, (b) suburban site Rebstockpark, and (c) urban study site no 1. White triangles indicate focal burrows within study sites.

Source: Google Earth.

bits inhabiting $n = 3$ different burrows located in the city center of Frankfurt (former rampart areas), $n = 4$ burrows at suburban sites located in the former periphery of the administrative district of Frankfurt, and $n = 3$ burrows located in adjacent rural areas (Table 1; Ziege et al. (2013, 2015, 2016) provided a detailed description of different degrees of urbanity for the respective study sites, as the degree of urbanity does not necessarily decrease continuously towards the outskirts of a city (McKinney, 2008). The investigated burrows harbored social rabbit groups consisting of eight to 15 individuals.

Behavioral observations

Activity patterns and time budgets

We asked whether European rabbit populations occurring along a rural-to-urban gradient differ in diurnal activity patterns and thus

quantified time spent outside their burrows (above-ground activity) and relative times allocated to different behaviors (i.e., time budgets, see below), respectively, in the course of the day. Behavioral observations were conducted between 27th September and 27th October 2011 (14 observation days) and between 11th June and 4th August 2012 (27 observation days) on three to four randomly selected days per week. The order by which the different burrows were observed was randomized. We divided the observation time into four sampling sessions that covered the entire day, starting one hour before sunrise and ending one hour after sunset. Each sampling session lasted between four and five hours, and two sampling sessions were usually performed on one day. In order to obtain comparable data for all three levels of urbanity, observational sessions for the period of the day were usually performed simultaneously by different observers at one rural, one urban and one suburban burrow. If this was not possible due to logistic constraints, the gap between data collection for the same time period of the day in different areas did not exceed more than two days. In total, we thus observed each rabbit group at least three times over the course of the entire day. We observed rabbits only during periods with no inclement weather.

The observers were sitting quietly at 50 m distance from the respective burrow and observed the area around the burrow entrances from two different angles. Upon arrival, and prior to data recording, the observers waited for 10 min (see Vosburgh and Irby, 1998). We used a scan sampling approach in combination with continuous focal animal sampling (Martin and Bateson, 1986). Every 15 min we noted numbers of rabbits, as well as pedestrians and dogs (leashed and unleashed), that were visible within a radius of 50 m around the focal burrow. Between the scans an adult focal animal was randomly selected and its behavior recorded for 15 min (or until the focal animal moved out of sight) using the program JWatcher v. 1.0 (Blumstein et al., 2006) operated on a transportable computer. For every 15 min observation period a new focal animal was chosen; an attempt was made to collect data from different individuals during each scan. However, since rabbits were not individually marked, we cannot exclude the possibility that some individuals were sampled repeatedly. Following Gibb (1993) and Magle and Angeloni (2011) we recorded the duration of the following behaviors or behavioral categories: (1) anti-predator behavior (*vigilance*: lifting head, ears straight, standing on the hind-feet; *flight behavior*: fast movement caused by disturbance), (2) digging, (3) grazing, (4) self-grooming, (5) moving (where individuals slowly change their position but do not flee from disturbance), (6) resting, and (7) social interactions (*amicable*: mutual grooming, playing, nose-to-nose contact; *agonistic*: biting, fighting, chasing).

Concealment from predation in burrows

We asked if there are differences between study sites in the use of the burrow as a refuge from predation and if rabbits in urban habitats re-emerge earlier from their burrow after a simulated predator attack than their rural counterparts. Between 14th April and 25th Mai 2012, one person approached the focal burrows from 50 m distance at a normal walking speed during dusk (between 7:00 and 9:30 p.m.). By moving in a spiral towards the center of the burrow and eventually crossing it, all rabbits close to the burrow were forced to enter the respective burrow. The observer then moved back to the observation spot at 25 m distance from the burrow and recorded the time until the first, second, etc. rabbit reappeared above ground. This time interval is henceforth referred to as the 'concealment time' (Adams et al., 1987). In addition to the above-mentioned $n = 3$ urban, $n = 4$ suburban and $n = 3$ rural burrow systems that had been observed in our assessment of activity patterns we additionally included another 11–12 burrow systems within the respective rural, suburban and urban study areas. Consequently, sample sizes for this experiment were $n = 15$

each for rural, suburban and urban groups. Observations lasted for 15 min, and if rabbits did not re-emerge within this time period, this ceiling value was noted as emergence time. All observations were performed by the same observer (S. Straskraba). Rabbits from each burrow were observed only once. The experiment was terminated when the observer was not able to force the rabbits underground. This was the case at most urban burrows, which had to be excluded from the analysis (see Results).

To investigate whether frequent human disturbance leads to a reduction of the time rabbits spend engaging in anti-predator behaviors, leading to shorter concealment times, we repeated the approach described above five times (with six to eight days between the repeated sampling) at $n=5$ randomly selected rural and $n=5$ suburban burrow systems.

Statistical analysis

Activity patterns and time budgets

All statistical analyses were conducted in SPSS version 13.0 for windows. First, we calculated the percentage of rabbits above ground for each burrow and focal scan by comparing numbers of rabbits observed above ground with the total number of rabbits occupying the respective burrow. Total numbers were obtained after our behavior observations during the regular hunting scheme using domestic ferrets (*Mustela putorius furo*) that chased rabbits out of their burrow (data were re-used from Ziege et al., 2015). We arcsine (square root)-transformed the relative data and used 'percent rabbits above ground' as the dependent variable in a linear mixed model (LMM, 'mixed procedure'). We used 'scan period (every 15 min observation period) nested within burrow ID' as a random factor. We categorized 'time passed since sunrise' in four categories: (1) ≤ 4 h after sunrise, (2) >4 h and ≤ 10 h, (3) >10 h and ≤ 16 h, and (4) >16 h after sunrise. The 'intensity of disturbance at the burrow' (cumulative numbers of dogs and humans within a perimeter of 50 m) was also categorized into four categories: (1) no disturbance, (2) low to medium disturbance (between 1 and 5 persons or dogs around the burrow), (3) medium disturbance (between 5 and 10 persons or dogs), and (4) high disturbance (>10 persons or dogs). We used 'urbanity' ($k=3$), 'time passed since sunrise' ($k=4$), and 'intensity of disturbance at burrow' ($k=4$) for each burrow and focal scan as explaining variables. We retained the interaction terms 'urbanity \times time passed since sunrise' and 'intensity of disturbance at burrow nested within urbanity' but excluded all other, non-significant interaction terms (all $P > 0.1$).

Second, we calculated the proportion of time rabbits spent engaging in different behaviors (anti-predator behavior, digging, grazing, self-grooming, moving, resting, social interactions). As rabbits spent only a small portion (less than 5%) of their time digging and self-grooming, we decided to combine these behaviors in one category ("other behaviors").

Our data-set of individual rabbit groups was zero-inflated (i.e., some behavioral categories were observed only sporadically), and so we decided to use the following statistical approach: We calculated mean values for each behavioral category in each 15 min observation period ($n=80$ time intervals) across rabbit groups, but for each of the three levels of urbanity separately. The resulting data sets for each behavioral category were compared between the three groups for similarity/dissimilarity using pairwise Spearman rank correlations with Bonferroni correction for alpha-error inflation due to multiple comparisons ($\alpha=0.05/3=0.017$). In this analysis, significant correlations between two data-sets (e.g., urban vs. rural) would suggest that populations show similar behavioral patterns.

Table 2

Results of a univariate LMM using 'percent rabbits above ground' [arcsine (square root)-transformed] as the dependent variable.

Fixed effects	F	df ₁ , df ₂	P
Urbanity	5.04	2, 1,086.58	0.01
Time passed since sunrise	52.59	3, 701.40	<0.01
Intensity of disturbance at burrow	14.33	3, 1,090.00	<0.01
Urbanity \times time passed since sunrise	5.82	6, 793.18	<0.01
Intensity of disturbance at burrow (urbanity)	2.53	6, 1,094.32	0.02
Covariance parameters			
	Estimate	SE	
V_{within}	0.105	0.005	
V_{between}	0.009	0.004	

Concealment from predation in burrows

As data were not normally distributed, we used a non-parametric Mann-Whitney *U*-test to test whether concealment times differed between rural and suburban rabbit populations. We considered (a) the shortest concealment time (first rabbit that reappeared above ground) and (b) the mean of the shortest and longest concealment times (from the last rabbit that reappeared above ground) for each burrow.

Moreover, we compared shortest concealment times during the repeated simulated predator attacks (repeated measurement) in a repeated measures general linear model (rmGLM) using 'test order' ($k=5$, see above) as a within-subjects factor and 'urbanity' as a between-subjects factor, including the interaction term 'test order \times urbanity'.

Results

General activity patterns

The percentage of rabbits that were active (i.e., encountered outside of their burrow) differed significantly among the three categories of study sites (factor 'urbanity' in Table 2). At suburban study sites, we found, on average, the highest percentage of rabbits outside their burrows (mean \pm SE = $21.8 \pm 1.4\%$, $n=384$ focal scans). High values of $18.0 \pm 1.3\%$ ($n=390$ focal scans) were also found at urban study sites, while only $12.2 \pm 1.2\%$ ($n=353$ focal scans) of rabbits were observed outside of their burrows at rural study sites.

Moreover, 'time passed since sunrise', 'intensity of disturbance at burrow' as well as the interaction terms 'urbanity \times time passed since sunrise' and 'intensity of disturbance at burrow nested within urbanity' had significant effects (Table 2). Rabbits at all study sites were most active in the early morning (≤ 4 h after sunrise), decreased activity around noon (>4 h and ≤ 10 h after sunrise), and spent increasingly more time outside their burrows starting again in the late afternoon (>10 h after sunrise; Fig. 2a). However, suburban and urban populations were more active above ground around noon and in the afternoon compared to their rural conspecifics (Fig. 2a). This resulted in a pattern where suburban and urban rabbits showed a less pronounced daytime rhythmicity than rural populations.

At rural sites, no disturbance by humans and dogs was observed in 52.2% of all focal scans, while this was the case in only 14.3% of scan sampling points at urban study sites and 37.4% for suburban study sites. In the city center, rabbits were twice as often (8.2%) exposed to high disturbance (>10 persons or dogs) at their burrows compared to rural (4.5%) or suburban rabbit populations (4.2%). We found the factors 'disturbance at the burrow' and 'disturbance at the burrow nested within urbanity' to predict activity patterns (Table 2). In general, we observed a gradual decrease of the rabbits' above-ground activity with increasing disturbance intensity (Fig. 2b); however, the response to disturbance was strongest in rural rabbit groups: even at high disturbance (>10 persons or dogs around the burrow), some rabbits belonging to the respective

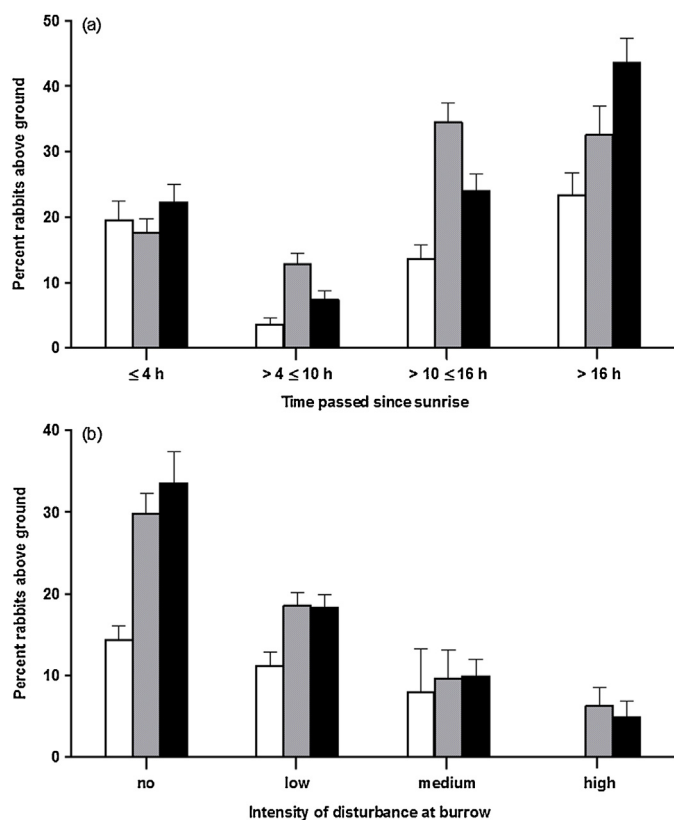


Fig. 2. Activity above ground.

Mean (\pm SE) percentage of rabbits above ground at rural (white), suburban (grey) and urban (black) sites with respect to (a) the time passed since sunrise and (b) different intensities of disturbance at the focal burrows (low disturbance: between 1 and 5 persons/dogs within 50 m around the burrow, medium disturbance: between 5 and 10 persons/dogs, high disturbance: >10 persons/dogs).

Table 3

Mean (\pm SE) proportions of time rabbits spent engaging in different behaviors at rural (6 h, 40 min of behavioral observations during $n = 121$ 15-min focal scans), suburban (16 h, 7 min, $n = 172$ focal scans) and urban study sites (16 h, 50 min, $n = 170$ focal scans).

Behavioral categories	Rural	Suburban	Urban
Anti-predator behavior	39.4 \pm 2.5	18.9 \pm 2.1	22.6 \pm 2.1
Grazing	40.5 \pm 3.2	54.4 \pm 2.8	45.6 \pm 2.6
Moving	6.7 \pm 1.4	6.9 \pm 1.2	12.6 \pm 1.2
Resting	9.4 \pm 2.4	15.5 \pm 2.0	15.7 \pm 2.1
Socio-positive interactions	0.8 \pm 0.3	0.5 \pm 0.2	0.3 \pm 0.2
Socio-negative interactions	0.4 \pm 0.4	0.6 \pm 0.2	0.6 \pm 0.2
Others	2.8 \pm 1.0	3.2 \pm 0.8	2.6 \pm 0.7

focal burrow were still observed above ground at suburban and urban sites, but this was not the case in rural rabbit populations (Fig. 2b). Even with no disturbance, only 14.3 \pm 1.8% of the rabbits per burrow were observed above ground at rural study sites, while urban (33.5 \pm 3.2%) and suburban (29.8 \pm 2.0%) rabbit populations were far more active (Fig. 2b).

Time budgets

An overview of time budgets at rural, suburban and urban sites is given in Table 3 and Fig. 3. Spearman rank correlations found statistically significant correlations between rural and suburban populations in anti-predator and grazing behavior, suggesting some degree of congruency in activity patterns between rural and suburban populations (Table 4; Fig. 3a,b). No significant correlations were found between data sets from rural and urban or

Table 4

Results of pairwise Spearman rank correlations for $n = 80$ sample points (averages across different groups at each level of urbanity; sample intervals were every 15 min from one hour before sunrise to one hour after sunset) for the different behavioral categories considered in this study. Significant effects (bold typeface) indicate congruency in diurnal activity patterns between groups from sites with different levels of urbanity.

Behavioral categories		Suburban	Urban
Anti-predator behavior	Rural	$r = 0.30, P = 0.01$	$r = -0.05, P = 0.67$
	Suburban		$r = 0.12, P = 0.30$
Grazing	Rural	$r = 0.45, P < 0.01$	$r = -0.03, P = 0.77$
	Suburban		$r = 0.10, P = 0.39$
Moving	Rural	$r = 0.10, P = 0.37$	$r = 0.08, P = 0.48$
	Suburban		$r = 0.08, P = 0.47$
Resting	Rural	$r = 0.02, P = 0.85$	$r = -0.07, P = 0.54$
	Suburban		$r = 0.06, P = 0.60$
Socio-Positive Interactions	Rural	$r = 0.08, P = 0.46$	$r = 0.01, P = 0.93$
	Suburban		$r = 0.01, P = 0.91$
Socio-Negative Interactions	Rural	$r = 0.19, P = 0.09$	$r = -0.08, P = 0.49$
	Suburban		$r = 0.05, P = 0.66$
Others	Rural	$r = 0.04, P = 0.75$	$r = -0.02, P = 0.89$
	Suburban		$r = 0.14, P = 0.22$

Table 5

Results from a rmGLM using shortest concealment times from the 1st to 5th simulated predator attacks as the dependent variable (repeated measurement, *rm*). Groups from rural and suburban sites are compared.

	Effect	df	Mean square	F	P
Within-subjects effects	Rm	4	113,940.83	3.70	0.01
	Rm \times urbanity	4	42,596.57	1.38	0.26
	Error	32	30,803.58		
Between-subjects effects	Urbanity	1	26,865.62	0.38	0.55
	Error	8	69,892.25		

between data-sets from suburban and urban sites (Tables 3 and 4; Fig. 3).

Concealment from predation in burrows

In our experiment on concealment times, a Mann-Whitney *U*-test detected no significant differences between rural and suburban study sites for the shortest concealment time [median (interquartile range), rural study sites: 165 s (97–311 s); suburban: 185 s (85–962 s); $z = -0.66, P = 0.51, n_1 = n_2 = 15$] and for the mean of the shortest and longest concealment time [rural study sites: 404 s (311–581 s); suburban: 554 s (356–741 s); $z = -1.47, P = 0.14, n_1 = n_2 = 15$]. Note, however, that we had to exclude urban study sites from this analysis: in 14 out of 15 burrows urban rabbits never entered the focal burrow and also did not enter any other burrow nearby, but merely avoided the source of disturbance by moving away above ground.

Finally, the rmGLM comparing shortest concealment times before and after repeated approaches by the observer detected a significant effect of the repeated measurement (Table 5), indicating that rabbits habituate to permanent anthropogenic disturbance by reducing the time spent in the burrow after disturbance (means \pm SE for fastest reappearance times at the rural study site: 1st = 336 \pm 128 s, 2nd = 174 \pm 99 s, 3rd = 147 \pm 41 s, 4th = 255 \pm 60 s, 5th = 196 \pm 85 s; suburban study site: 1st = 478 \pm 128 s, 2nd = 367 \pm 99 s, 3rd = 88 \pm 41 s, 4th = 141 \pm 60 s, 5th = 265 \pm 85 s). We found no significant effect of the interaction term 'repeated measures \times urbanity' and no main effect of 'urbanity' (Table 5).

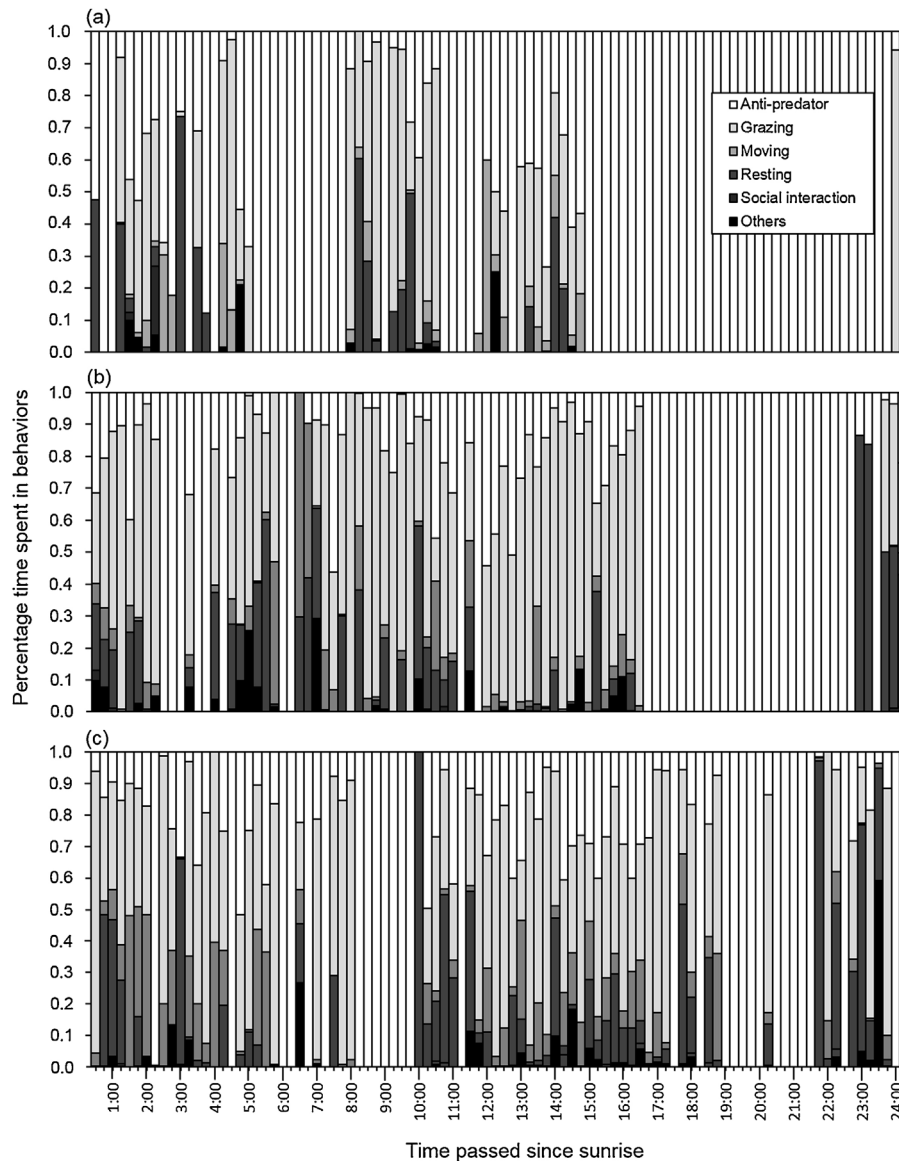


Fig. 3. Time budgets.

Time budgets of rabbits at (a) rural, (b) suburban, and (c) urban study sites in and around Frankfurt a.M. in Germany. Shown are percentage proportions of anti-predator behaviors (including time spent inside burrows), grazing, moving, resting, social interactions and other behaviors (self-grooming and digging) for every 15 min sampling interval after sunrise.

Discussion

General activity patterns and time budgets

Generally, our results largely confirm previous studies on behavioral changes of synanthropic species in response to altered predation regimes in today's modern cities (fox squirrels: [McCleery, 2009](#); black-tailed prairie dogs: [Magle and Angeloni, 2011](#); cape ground squirrels: [Chapman et al., 2012](#); but see [Ryan and Partan, 2014](#) for review of contrasting studies).

Especially in our suburban study sites (Figs. 2b, 3b), rabbits were active above ground even during times when this species tends to be underground and less active in other areas ([Gibb, 1993](#); [von Holst et al., 1999](#); [Moseby et al., 2005](#)). We suggest that suburban rabbit populations benefit twofold from these behavioral changes compared to rural and urban rabbit populations: (a) although we did not quantify actual predation risk, we argue that suburban populations are likely to experience less predation pressure by natural predators compared to rural sites ([Ryan and Partan, 2014](#)) and less

intense disturbance by humans compared to urban study sites. In our suburban study sites the intensity of anthropogenic disturbance at burrows was comparable to that observed at the rural study sites (see also [Ziege et al., 2015, 2016](#)). Instead of investing in anti-predator behaviors, suburban rabbits spend more time grazing and resting (Table 3; Fig. 3). Our findings correspond well with the study of [Chapman et al. \(2012\)](#) who found “peri-urban” populations of Cape ground squirrels to also invest most of their time spent above ground in grazing during summer. However, the authors also noted that at their peri-urban study site the availability of food sources was lower compared to the urban study site and thus, animals had to invest more time into foraging than their urban conspecifics. In our study area, no evidence suggests that access to food sources at suburban sites would be lower compared to urban ones.

Urban rabbits invested twice as much time into moving compared to rural or suburban rabbits (Table 3; Fig. 3), which we interpret as a strategy to avoid permanent human disturbance. This is further supported by the fact that we were not able to force rabbits underground during the concealment experiment but animals

rather avoided the disturbance above ground by dogging a humans' approach (see below). In a previous study, Ziege et al. (2013) found the shortest flight initiation distances at urban sites, but significantly longer distances at suburban and rural sites, confirming the hypothesis that urban rabbits are well habituated to human nuisance. However, during highest intensities of human presence [e.g., when citizens go to (>4 h ≤ 10 h after sunrise) and return from work (>10 h and ≤ 16 h after sunrise)] urban rabbits mostly reside within their burrows, while at suburban sites rabbits were still seen outside their burrows at these times (Figs. 2 and 3).

As predicted, rural rabbits showed the highest percentage of anti-predator behavior, which is congruent with the idea that the predation risk by natural predators is higher compared to suburban and urban sites. We were more often able to observe common predators, such as foxes or birds of prey (kestrels, *Falco tinnunculus* and sparrow hawks, *Accipiter nisus*) at our rural studies. In addition, free-ranging domesticated dogs and cats were occasionally observed. This corresponds with longest flight initiation distances reported by Ziege et al. (2013) for the rural rabbit populations considered here. Interestingly, our study found more socio-negative interactions in suburban and urban rabbit populations compared to rural ones. In accordance with other studies (for review see Ryan and Partan, 2014) we suggest that higher rabbit population densities at our suburban and urban sites lead to higher competition, which in turn triggers a higher degree of intra-specific aggression, e.g., in the form of territorial behavior (compare Ziege et al., 2016). Beside differences in predation pressure between urban, suburban and rural study sites we argue that shifts in climatic conditions may also contribute to the observed results. For example, mean temperatures are usually higher inside cities compared to the rural outskirts (Pickett et al., 2001). This may cause urban and suburban rabbit populations to leave their burrows earlier in the morning and enter them later in the evening, respectively (see also Brivio et al., 2016).

Concealment from predation in burrow

We hypothesized that urban and suburban rabbits should have shorter concealment times (time needed to reappear above ground after disturbance) compared to rabbits at rural sites (Adams et al., 1987). For urban rabbits we could show that they are well habituated to human-induced disturbance (see above). However, we did not find differences in concealment times between rural and suburban sites. Likewise, repeated human disturbance led to a habituation response, but again, no differences between rural and suburban sites were detected. Possibly, the differences in disturbance rates were not strong enough to cause measurable behavioral differences. On the one hand, our classification as 'rural' does obviously not correspond to the complete absence of humans; on the other hand, burrows at our suburban study sites were mostly located within bushes at the periphery of parks, while pathways used by humans are usually located more in the center of parks.

Conclusions

Our study provides another example of the remarkable ability of certain wildlife species to habituate to (and even flourish under) altered environmental conditions in urban and suburban regions. This paper highlights differences in behavioral responses to human presence and predation risk in urban and suburban environments as drivers of advantageous shifts in activity patterns. In case of the European rabbit, suburban areas in particular serve as suitable habitats and may soon play a vital role in the conservation of this species that was once common in Europe.

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