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Original investigation

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.

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).

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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 quirrels: 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* (Duduś 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-