Effects of gradual anthropogenic habitat alteration on the ecology and behavior of European rabbits (*Oryctolagus cuniculus*) in and around Frankfurt am Main

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Summary

The process of urbanization is one of the major causes of the global loss of biodiversity; however, cities nowadays also have the potential to serve as new habitats for wildlife. The many-fold forms of land use in urban areas provide a variety of ecological niches, even for plant and animal species that were formerly assumed to be absent from cities. A milder microclimate and the higher consistency in resource availability within the urban environment (e. g., food or nest sites) are known to reduce migratory behavior, prolong breeding seasons and increase longevity in birds, mammals or reptiles. A lower predation pressure further favors high population densities of some species within cities, at times for even causing human-wildlife conflicts. Nevertheless, within the urban environment, anthropogenic impact reaches its maximum and only organisms that are able to adapt to the urban-specific abiotic and biotic conditions (e. g., the permanent presence of humans) can successfully establish populations. Therefore, a key question of urban ecology is what mechanisms underlie the observation that some species become "urban exploiters" and "urban tolerants" whereas others are classified as "urban avoiders" or "urban impossibles".

The European rabbit (*Oryctolagus cuniculus*, L. 1758) is a typical example of a wildlife species that reaches stable population densities in cities. Due to intense plant and soil damages, German city authorities aim to control high rabbit densities through the application of a yearly hunting regime (e. g., in Munich, Berlin or Frankfurt am Main). In contrast, the spread of the virus diseases Myxomatosis in 1952 and Rabbit Hemorrhagic Disease (RHD) in the begin of 1980 led to declining population densities of *O. cuniculus* in German rural areas, i. e., numbers of yearly hunting bags decreased.

The aim of my doctoral thesis was to answer the following research questions: Do population densities of the European rabbit correlate with the intensity of urbanization in and around Frankfurt am Main and if so, which factors play a role in varying densities? How are burrow construction behaviors and group sizes, daytime activity patterns and anti-predator behaviors as well as communication behaviors of this mammal affected by urbanization? My research on the effects of gradual anthropogenic habitat alteration on the ecology and behavior of *O. cuniculus* aimed not only to enlarge knowledge to the yet young research field of urban ecology. In cooperation with the city council of Frankfurt, hunters and associations for ecological conservation contributions ought to be made to the development of management tools that are needed to control for wildlife population dynamics on a long-term scale, not only for rabbits.

In my first study in Chapter 2, I focused on population dynamics across 17 different study sites in and around Frankfurt. To collect reliable data on rabbit densities within study sites that differ in their vegetation heights and thus, the probability to detect the animals, I used a combination of methods. In addition to repeated direct census counts along pre-defined transects during dusk and dawn I further assessed burrow densities and performed direct observations at burrows. As one of yet few studies, I invented an approach that quantified the intensity of urbanization (degree of urbanity) of each study site base on four variables: (1) intensity of anthropogenic disturbance per min and ha, (2) number of residents within a radius of 500 m, (3) proportion of artificial ground cover and (4) numbers of anthropogenic objects per ha. To account for behavioral adaptations in response to human disturbance, I measured flight initiation distances (FIDs, i. e., the distance to which a human can approach before an animal starts altering its behavior). Spearman rank correlations confirmed that with increasing degree of urbanity also rabbit and burrow densities increased. At the same time, FIDs decreased along the rural-to-urban gradient which demonstrates that urban populations are especially highly habituated to human disturbances. The access to dense shrubs, bushes etc. as suitable sites for burrow construction is the most determining factor for rabbit abundances, and therefore I presumed different densities along the rural-to-urban gradient to be driven by shifts in the availability of thick vegetation. I argued, that in areas with diverse landscape patterns that alternate on a small scale – as typical for the urban and suburban matrix – sites suitable for burrow construction are highly available. In contrast, rural areas are mostly agriculturally transformed, open landscapes where dense vegetation is scarce. Moreover, food sources seem to become more abundant with increasing degree of urbanity and further favor high densities of *O. cuniculus* in the city center of Frankfurt.

The study presented in Chapter 3 focused on burrow characteristics and rabbit group sizes within study sites as clear indicators for differences in habitat quality. In areas where suitable sites for burrow construction are not limited, burrows of *O. cuniculus* are known to be often evenly distributed, to have fewer entrance holes and to host smaller groups. Base on the burrows' coordinates, I calculated two indices that in both cases classified burrows to be either accumulated, evenly or randomly distributed within study sites. Additionally, in cooperation with local hunters the number of burrow entrances and animals that occupy the same burrow had been determined during the hunting season (October till March). A total of 61 burrows were randomly selected along the rural-to-urban gradient for an in-depth analysis of external burrow structures (e. g., measurement of distances between entrances). With increasing degree of urbanity burrow distribution patterns shifted from accumulated in rural areas towards more evenly distributed within the city center of Frankfurt. This is a clear sign for an increasing access to sites suitable for burrow construction along the rural-to-urban gradient.

As argued in my first study, rural areas are nowadays mostly homogenous landscapes with limited access to dense vegetation whereas suburban and urban gardens, parks etc. offer rabbits a variety of sites where burrows can be established. Additional Spearman rank correlations revealed that the external dimensions of burrows decreased (shorter distances between entrances) and that burrows became less complex (fewer entrances) along the rural-to-urban gradient. In accordance, the number of rabbits that commonly shared the same burrow system was highest within rural areas, whereas I found mainly pairs and single individuals within highly urbanized study sites. In addition to differences in the availability of resources (dense vegetation etc.), I suggested that habitat fragmentation and a reduced predation pressure within the urban environment further cause burrows to have fewer entrances and to host smaller groups. I addressed varying predation pressures within study sites in my third study.

In cities, anthropogenic disturbance reaches its maximum whereas predation pressure seems to be lower compared to the rural environment. The quantification of predation within a habitat has proven to be difficult to measure; therefore, in my study I instead measured the amount of time prey species spend on anti-predator-behaviors, such as concealing themselves underground. The publication in Chapter 4 compared activity patterns, burrow use and percentages of anti-predator behaviors from one hour before sunrise until one hour after sunset of rural, suburban and urban rabbit groups. Moreover, direct anthropogenic disturbance at burrows was quantified; i. e., pedestrians and dogs were counted. Decreasing FIDs along the rural-to-urban gradient led to the assumption that the percentage of time rabbits spend on anti-predator-behaviors (e. g., concealing themselves in the burrow) is lowest within urban populations. A linear mixed model (LMM) and Spearman rank correlations confirmed my hypothesis: Animals located at urban and suburban sites spent, on average, more time outside their protective burrows compared to their rural conspecifics. At suburban sites, individuals invested the least amount of time in anti-predator behavior but most interestingly, I found urban rabbits to invest twice as much time into above ground moving compared to rural or suburban rabbits. I interpreted this observation as the animals' strategy to avoid permanent human disturbance, which was highest at urban burrows. This assumption was confirmed experimentally by chasing the members of different social groups into their burrows: In only one trial out of 15 I was able to chase rabbits at urban sites into their burrow whereas at suburban and rural study sites all rabbits concealed themselves underground in response to the human approach. Conclusively, results of this third study gave evidence that suburban rabbit populations on one hand benefit from less predation pressure by natural predators in comparison to rural sites, whereas on the other hand are exposed to less intense disturbance by humans compared to urban study sites.

The last study presented in Chapter 5 focused on the effects that urbanization had on the latrine-based communication behavior of rabbits. As many other mammals, *O. cuniculus* exchange information via the deposition of excreta in latrines, and depending on the intended receiver(s), latrines are either formed in central areas for within-group communication or at territorial boundaries, e. g., for between-group communication. The relative importance of within- vs. between-group communication depends on, amongst other factors, population densities and group sizes which I proved both to shift along the considered rural-to-urban gradient. I determined latrine sizes, latrine densities and latrine utilization frequencies relative to their distance to the nearest burrow at 15 different study sites. I predicted that peripheral marking for territorial defense is more important in urbanized regions, as increasing population densities lead to higher intraspecific competition, e. g., for territorial space. Moreover, small group sizes at urban study sites should also favor peripheral over core marking behavior as the necessity to communicate within groups decreases. Indeed, latrine densities and utilization frequencies increased with increasing distance from the burrow in suburban and urban populations whereas at rural sites, largest latrines and those containing the most fecal pellets were close to the burrow, suggesting that within-group communication prevailed. Relaxed predation pressure within urban sites and a higher availability of shelter-providing structures allowed the animals to frequently use latrines at the periphery of their protective burrows compared to rural populations. Shorter distances between latrines and woody vegetation within urban areas were finally another indicator for my main argumentation, that urban areas offer a more heterogeneous landscape as it is the case at rural habitats.

To sum up, for the first time, I was able to relate shifts in the ecology and behavior of the European rabbit as adaptations to a gradual anthropogenic habitat alteration that are typical for "urban exploiters". An important outcome of my research was it's relevance to the framework of sustainable population management plans in urban and rural landscapes; not only for rabbits, but also for other species with similar habitat requirements that are on decline in Germany. The suburban habitat provides high landscape heterogeneity ("edge habitat") and comparably low human disturbance and predation pressure in contrast to the agriculturally transformed, open landscapes which are nowadays typical for most rural areas in central Europe. One of my initial questions was, why rabbit populations in German rural areas are on decline, whereas densities are high in cities. Through the quantification of the intensity of urbanization, I added knowledge to this question, specifically in my publications on changes of burrow characteristics and latrine-based communication networks of *O. cuniculus* along a rural-to-urban gradient where I demonstrated how urbanization can directly and indirectly affect wildlife on various ecological aspects.

Zusammenfassung

Die Zerstörung natürlicher Lebensräume während des Prozesses der Urbanisierung gilt als einer der Hauptgründe für den Verlust der globalen Artenvielfalt. Dem gegenüber steht die Beobachtung, dass moderne Städte durchaus alternative Lebensräume für Tier- und Pflanzenarten bieten. Neben den zahlreichen freien ökologischen Nischen, die aus einer vielfältigen Habitatnutzung hervorgehen, zeichnet sich das urbane Ökosystem vor allem durch einen konstant hohen Zugang zu Ressourcen aus (z. B. Nahrung oder Nistplätze). Das generell wärmere Mikroklima und ein oft geringerer Prädations- und Jagddruck führen weiterhin dazu, dass viele in Städten lebende Arten höhere Populationsdichten erreichen als ihre Artgenossen auf dem Land. Der urbane Lebensraum stellt jedoch eine anthropogen geprägte selektive Umgebung dar, in der solche Individuen bessere Überlebenschancen haben, die flexibel auf die neuartigen Bedingungen wie z. B. der ständigen Präsenz des Menschen reagieren. Kernfragen des Forschungsgebietes der Stadtökologie sind somit, warum einige Arten Städte als neue Lebensräume nutzen und dort hohe Populationsdichten erreichen („urban exploiter“), während andere dazu nicht in der Lage sind und nur selten bzw. nie in urbanen und suburbanen Räume vorkommen („urban impossibles“). Bisher konnte nur ansatzweise für wenige Arten geklärt werden, welche Folgen das Leben in der Stadt auf deren Ökologie und Verhalten hat.

Das Europäische Wildkaninchen (*Oryctolagus cuniculus*, L. 1758) ist ein typisches Beispiel für eine Wildtierart, die hohe Populationsdichten in städtischen Arealen wie Parkanlagen oder Friedhöfen erreicht und Schäden an Bepflanzungen etc. verursacht. Häufig kommt es daher insbesondere in Großstädten wie Berlin, München oder Frankfurt am Main zu Konflikten mit der urbanen Bevölkerung, so dass Jagdmaßnahmen zur Dezimierung der Kaninchenbestände ergriffen werden. Im Gegensatz dazu ist mit Auftreten der Viruserkrankungen Myxomatose im Jahre 1952 bzw. der Chinaseuche (Rabbit Hemorrhagic Disease, RHD) in den 1980er Jahren eine deutliche Abnahme der Bestände in ländlichen Gegenden Deutschlands zu beobachten.

Ziel meiner publikationsbasierten Doktorarbeit war es am Beispiel von Frankfurt am Main und Umgebung folgende Fragestellungen zu beantworten: Gibt es tatsächlich einen Zusammenhang zwischen dem Grad der Urbanisierung und den Populationsdynamiken von *O. cuniculus* und wenn ja, welche Faktoren liegen einer unterschiedlichen Bestandsentwicklung zu Grunde? Welchen direkten und indirekten Einfluss hat der Grad der Urbanisierung auf die Bautenanlage und Gruppengröße, die Tagesaktivität und das Anti-Prädator-Verhalten sowie das Kommunikationsverhalten

dieser Säugetierart? Der Anspruch meiner Arbeit bestand nicht nur darin zur Schaffung von Grundlagenwissen innerhalb des noch jungen Forschungsbereiches der Stadtökologie beizutragen. In enger Zusammenarbeit mit der Stadtverwaltung Frankfurt, mit Jägern und Naturschutzvereinen sollten die aus meiner Feldarbeit gewonnenen Ergebnisse zur Ökologie und zu den adaptiven Verhaltensweisen einer Wildtierart entlang eines rural-urbanen Gradienten direkte Anwendung im Natur- und Artenschutz finden, z. B. um künftige Entscheidungen hinsichtlich eines nachhaltigen Wildtiermanagements zu erleichtern.

In meiner ersten Studie wurden zunächst die Populations- und Bautendichten von Wildkaninchenpopulationen in insgesamt 17 verschiedenen Studiengebieten innerhalb der Frankfurter Innenstadt, den Parkbereichen der näheren Umgebung des Stadtzentrums bzw. in rural angrenzenden, landwirtschaftlich genutzten Gebieten erfasst (Kapitel 2). Da die Sichtungswahrscheinlichkeit von Wildkaninchen in unterschiedlichen Habitaten variieren kann, wurden für eine zuverlässige Bestandsabschätzungen entlang des rural-urbanen Gradienten mehrere Ansätze gewählt. Neben der wiederholten Transektzählung mit Handscheinwerfern in der Dämmerung wurde auch die Anzahl der Bauten pro ha erfasst sowie direkte Zählungen an den Bauten vorgenommen. Als eine von bisher sehr wenigen Studien bezog meine Arbeit lokale Unterschiede im Grad der Urbanisierung zwischen diesen Gebieten in die statistischen Analysen mit ein. So wurde für jedes Gebiet ein Urbanitätsindex berechnet, der auf folgenden Variablen basiert: (1) die Störungsintensität durch den Menschen pro ha und min, (2) die Einwohnerdichte in 500 m Umkreis vom Studiengebiet, (3) dem prozentualen Anteil versiegelter Oberflächen (Gebäude, Straßen etc.) sowie (4) die Anzahl anthropogener Gegenstände pro ha. Das Messen der Fluchtinitiationsdistanz (FID) als die Distanz, auf die sich ein Mensch einem Wildtier annähern kann bevor es die Flucht ergreift, sollte zudem Aufschluss über die Anpassungsfähigkeit von *O. cuniculus* gegenüber anthropogenen Störungen geben. Mittels einer Spearman-Rangkorrelation konnte gezeigt werden, dass die Populations- sowie Bautendichten mit steigendem Grad an Urbanität signifikant zunahmen. Gleichzeitig zeigte eine Abnahme der FIDs entlang des rural-urbanen Gradienten, dass insbesondere Tiere in der Innenstadt an die stetige menschliche Präsenz angepasst sind. Populationsdichten des Wildkaninchens werden maßgeblich vom Vorhandensein dichter Vegetation zur Anlage von Bauten bestimmt. Hohe Bestände finden sich in mosaikartigen Landschaften, in denen der Zugang zu Hecken, Büschen etc. vorhanden ist. Solche Landschaftsstrukturen sind typisch für städtische Gebiete während sich rurale Lebensräume im Zuge der modernen agrarwirtschaftlichen Nutzung überwiegend durch Offenlandschaften auszeichnen. Zunehmende Kaninchendichten entlang des rural-urbanen Gradienten führte ich somit maßgeblich auf Unterschiede im Zugang zu dichter Vegetation sowie Nahrung zwischen den Studiengebieten zurück.

Wildkaninchen legen ihre Bauten bevorzugt in dichter Vegetation an – in Gebieten, wo diese Ressource nicht limitiert ist, sind Bauten gleichmäßiger verteilt, weisen wenige Eingänge auf und beherbergen meist kleine Kaninchengruppen. In Kapitel 3 präsentiere ich meine zweite Studie, in der ich die Verteilung und externe Struktur der Bautensysteme sowie die Gruppengröße der Tiere als Indikatoren für die Qualität des Habitats (z. B. Verfügbarkeit von dichter Vegetation, Prädationsdruck etc.) in den Studiengebieten untersuchte. Basierend auf den Daten zur Bautendichte wurden zwei Indices berechnet, die Aufschluss über die räumliche Verteilung der Bautensysteme innerhalb der Studiengebiete gaben (geklumpt, gleichmäßig, zufällig). Die Anzahl der Bautenöffnungen bzw. der Kaninchen pro Bau wurde während der Jagdsaison von Oktober bis März in Kooperation mit Stadtjägern bestimmt. Weiterhin wurden insgesamt 61 zufällig ausgewählte Bauten entlang des rural-urbanen Gradienten oberirdisch vermessen, z. B. die Distanz der Öffnungen zueinander erfasst. Mit zunehmendem Grad der Urbanisierung konnte eine gleichmäßigere Verteilung der Kaninchenbauten beobachtet werden – ein eindeutiger Hinweis dafür, dass entlang des rural-urbanen Gradienten die Anzahl an Strukturen zur Anlage von Bauten zunimmt. Weiterhin nahm die Anzahl der Ein- und Ausgänge sowie die oberirdische Ausdehnung der Bauten mit zunehmendem Grad der Urbanisierung signifikant ab. So dominierten in der Frankfurter Innenstadt kleine Bauten mit wenigen Ein- und Ausgängen die wiederum von nur wenigen Tieren bewohnt waren, oft sogar nur von Pärchen oder einzelnen Wildkaninchen. Im ländlichen Umland Frankfurts hingegen wiesen die Bautensysteme deutlich mehr Öffnungen auf welche sich zudem in größeren Abständen voneinander befanden. Diese Bauten wurden vorwiegend von großen Kaninchengruppen bewohnt. Die ländlichen Studiengebiete zeichneten sich durch offene, vorwiegend intensiv agrarwirtschaftlich genutzte Flächen aus, in denen es nur wenig dichte Vegetation gibt. Im Gegensatz dazu bieten die vielfältigen Landnutzungsformen in der Stadt ausreichend Möglichkeiten zur Anlage von Bauten. Gleichzeitig scheint jedoch die Habitatfragmentierung durch Straßen und Wege ein Grund dafür zu sein, warum die oberirdische Ausdehnung der Bauten in den urbanen Studiengebieten limitiert ist. Ein weiterer wichtiger Faktor, der sowohl die Unterschiede in den Populationsdichten sowie die Anlage von Bauten mit weniger Öffnungen und die Formation kleinerer Gruppen zwischen Stadt und Land erklärt, ist der Prädationsdruck. Dieser Aspekt war im Fokus meiner dritten Studie.

In Städten ist die Störung durch den Menschen besonders intensiv während viele Studien darauf hinweisen, dass die Häufigkeit der Prädation durch natürliche Beutegreifer oft geringer ist. Da sich die Intensität der Prädation innerhalb eines Gebietes jedoch nur sehr schwer quantifizieren lässt wird als Indikator für den Prädationsdruck häufig die Zeit gemessen, die das Beutetier in „Anti-Prädator-Verhalten“ investiert. So sind Wildkaninchen in ihren natürlichen Lebensräumen vorwiegend dämmerungsaktiv und nutzen regelmäßig den Bau, um sich vor Fressfeinden in Sicherheit zu bringen. Kapitel 4 umfasst eine Publikation, in der ich Unterschiede in den Tagesaktivitäten und im Baunutzungsverhalten sowie im Anti-Prädator-Verhalten ruraler, suburbaner und urbaner Wildkaninchengruppen untersuchte. Verhaltensbeobachtungen an jeweils 4 urbanen, suburbanen und ruralen Bauten fanden von einer Stunde vor Sonnenaufgang bis einer Stunde nach Sonnenuntergang statt. Gleichzeitige wurde die anthropogene Störungen an den Bauten quantifiziert und alle Fußgänger bzw. Hunde in regelmäßigen Abständen gezählt. Ein „linear mixed model" (LMM) und Rangkorrelationen nach Spearman bestätigten, dass sich Tiere in den urbanen und suburbanen Studiengebieten signifikant öfter außerhalb des Baues aufhielten als ihre ruralen Artgenossen. Weiterhin ergab die Studie, dass ländliche Wildkaninchen 40 % ihrer Zeit darin investierten, nach Fressfeinden Ausschau zu halten sobald sie den Bau verließen. In den urbanen und suburbanen Studiengebieten nahm diese Verhaltensweise nur 20 % der Tagesaktivität der Tiere ein. Statt der „Überwachung" ihrer Umgebung verbrachten städtische Wildkaninchen mehr Zeit damit, Nahrung aufzunehmen oder sich auszuruhen. Interessant ist, dass die Tiere in der Frankfurter Innenstadt besonders oft ihren Standort zu den Tageszeiten wechselten, an denen Fußgänger zur Arbeit gehen bzw. von der Arbeit kommen. Dieses stetige Bewegungsverhalten interpretierte ich als eine Anpassung von *O. cuniculus* an die in den urbanen Gebieten doppelt so intensive Störung durch den Menschen im Vergleich zu den suburbanen und ruralen Studiengebieten. Diese Annahme wurde durch einen weiteren Feldversuch bestätigt, in dem ich mittels eines simulierten Beutegreiferangriffes versuchte, Wildkaninchen in ihren Bau zu treiben. Während in den ruralen und suburbanen Studiengebieten alle Tiere vor dem vermeintlichen Feindangriff unterirdischen Schutz aufsuchten, gelang es mir in 14 von 15 Versuchen nicht, urbane Tiere in den Bau zu treiben. Die Ergebnisse dieser Untersuchung führten zu der Schlussfolgerung, dass Wildkaninchen in den suburbanen Studiengebieten nicht nur einem geringeren Prädationsdruck im Vergleich zu den ländlichen Gebieten ausgesetzt; auch die Störung durch den Menschen ist weniger intensiv im Vergleich zur Frankfurter Innenstadt.

Im letzten Kapitel 5 untersuchte ich den Einfluss der Urbanisierung auf das Kommunikationsverhalten des Wildkaninchens. Wie bei vielen anderen Säugetierarten spielt auch bei *O. cuniculus* die Anlage von Kotanhäufungen (Latrinen) als olfaktorische und visuelle Signale für die Kommunikation eine große Rolle. So werden über die Duftstoffe, die sich im Urin bzw. im Kot befinden, während der gemeinsamen Nutzung der Latrinen Informationen über das Alter, Geschlecht oder den sozialen Status eines jeden Tieres ausgetauscht. Latrinen, die in nächster Nähe des Kaninchenbaus angelegt werden dienen insbesondere dem Informationsaustausch innerhalb derselben sozialen Gruppe. Latrinen hingegen, die in einiger Entfernung vom Kaninchenbau an den Grenzen des Territoriums angelegt werden, bilden einen olfaktorischen „Zaun" zu benachbarten sozialen Gruppen. Die aus den vorangegangenen Studien in Kapitel 2 und 3 gewonnenen Erkenntnisse ließen die Annahme zu, dass es eine Verschiebung der Latrinennetzwerke entlang des rural-urbanen Gradienten gibt: In den ruralen Studiengebieten dominieren große soziale Kaninchengruppen in großen Bautensystemen, die Dichte an Bauten bzw. Kaninchen ist hier jedoch gering. Folglich sollte die Kommunikation innerhalb derselben sozialen Gruppe durch Latrinen nah am Bau von größerer Wichtigkeit sein als die Abgrenzung zum weit entfernten Nachbar. In der Frankfurter Innenstadt hingegen, wo die Bauten- und Kaninchendichte sehr hoch ist und somit die Konkurrenz um Ressourcen, ist eine klare Abgrenzung zum Nachbarn durch periphere Latrinen von besonders großer Bedeutung. Weiterhin ist die „interne" Kommunikation in einer ohnehin kleinen sozialen Gruppe weniger wichtig. Die Analyse der Latrinenverteilungen bzw. Latrineneigenschaften (z. B. Anzahl Pellets, Dichte, Distanz zur nächsten Vegetation) entlang des rural-urbanen Gradienten bestätigte meine Hypothese. Wildkaninchen im ruralen Umland legten nicht nur die meisten Latrinen in direkter Nähe zum Bau an, diese wurden auch häufiger aufgesucht als Latrinen, die sich an den territorialen Grenzen befanden. Mit zunehmender Urbanisierung kam es zu einer Verschiebung der Latrinenverteilung. So befanden sich in der Frankfurter Innenstadt nicht nur besonders viele Latrinen an den Territoriumsgrenzen in einigen Metern entfernt vom Bau, sondern waren an diesen Latrinen auch häufiger Anzeichen einer regelmäßigen Nutzung (frische Kotpellets) zu finden als an solchen direkt am Bau. Die Anlage von Latrinen zur Kommunikation zwischen benachbarten sozialen Gruppen, z. B. um das Territorium eindeutig abzugrenzen, scheint somit bei Tieren in der Innenstadt besonders wichtig zu sein. Abschließend lieferte auch diese letzte Studie eindeutige Hinweise für meine Argumentation, dass es in suburbanen und urbanen Studiengebieten ausreichend dichte Vegetation in nächster Nähe zum Bau gibt bzw. ein geringerer Prädationsdruck vorliegt als im ruralen Umland. So nahm die Distanz der Latrinen zur nächsten Vegetation mit zunehmenden Grad der Urbanisierung ab und Kaninchen in der Innenstadt können auch bei der Nutzung peripher gelegener Latrinen schnell Schutz in angrenzender Vegetation aufsuchen.

Zusammenfassend trugen die Erkenntnisse aus meiner Forschungsarbeit zu einem besseren Verständnis bei, welchen direkten und indirekten Einfluss Urbanisierung auf die Ökologie und das Verhalten eines Wildtieres haben kann. Durch die Quantifizierung des Grades der Urbanität war es mir erstmals möglich Anpassungen im Baunutzungs- und Kommunikationsverhalten einer Säugetierart entlang eines rural-urbanen Gradienten nachzuweisen. Insbesondere die umfangreichen Feldarbeiten zu den Tagesaktivitäten bestätigten, dass Kaninchenpopulationen in Frankfurt die für „urban exploiter" typischen Verhaltensanpassungen wie z. B. ein reduziertes Anti-Prädator-Verhalten zeigen. Eine wichtige Erkenntnis meiner Arbeit ist, dass der suburbane Lebensraum besonders gut den Habitatansprüchen von *O. cuniculus* entspricht: Die vielfältige Habitatnutzung in den weitläufigen Parkbereichen gewährleistet nicht nur Zugang zu schützender Vegetation und Nahrung in nächster Nähe zueinander. Im Gegensatz zu den ländlichen Gebieten ist ein geringerer Prädationsdruck durch natürliche Beutegreifer wahrscheinlich während die Störung durch den Menschen weniger intensiv ist im Vergleich zur Innenstadt. Diese Beobachtung ist auch für das Populationsmanagement von Arten von Bedeutung, die ähnliche Habitatansprüche wie das Europäische Wildkaninchen haben und in ländlichen Gebieten Deutschlands zunehmend seltener vorkommen.

Preface

This doctoral thesis bases upon scientific field work I conducted within the last five years at the Institute of Ecology, Evolution and Diversity of the Goethe University Frankfurt. In accordance with the prerequisites of a cumulative (publication-based) dissertation, I first give an introduction into the main topic in Chapter 1, namely the effects of urbanization on the ecology and behavior of wildlife. This Chapter 1 comprises the results and a critical discussion for each of my studies, followed by conclusive remarks on my work as a whole and additional data.

Accordingly, in Chapters 2-5 the respective manuscripts are attached which are all published in peer-reviewed (inter)national journals. In Chapter 2, I present results of the first study that accounted for European rabbit population dynamics along the rural-to-urban gradient. The degree of urbanization was positively linked with rabbit and burrow densities which suggest this species to be an "urban exploiter". A publication that demonstrated burrows and group sizes to become smaller with increasing degree of urbanity is provided in Chapter 3. This study was covered by the media worldwide after publication (for details see my Curriculum Vitæ). Moreover, I suggested differences in activity patterns and anti-predator behaviors of urban, suburban and rural rabbit populations to be caused by differences in habitat characteristics, e. g., the intensity of predation (Chapter 4). Finally, another study that was in the focus of the local press found shifts in latrine-based communication networks of rabbit populations located along the rural-to-urban gradient. This last research project demonstrated especially how urbanization can directly and indirectly influence the ecology and behavior of wildlife.

My contributions to the included publications are highlighted at the beginning of each chapter. While all publications represent a cooperative achievement combining the expertise of my own person and other scientists (as indicated by the author contributions), I use the 1st person singular during the introductive Chapter 1. For copyright reasons, I refrained from changing the journal-specific formatting style.

During the time I conducted my thesis, I was additionally involved in other projects (see my Curriculum Vitæ). I analyzed data on mate choice and latrine-based marking behavior in Arabian gazelles as well as provided scientific illustrations.

Chapter 1

An introduction into the effects of urbanization on the ecology and behavior of wildlife.

by Madlen Ziege

Anthropogenic habitat alteration, spread of species and diseases, input of pollutants and climatic changes are regarded as the factors with the most negative influence on natural environments which reach their maximum impacts through the process of urbanization (McDonald et al. 2008; Pickett et al. 2008, 2011; Shulenberger et al. 2008; reviewed in Rodewald & Gehrt 2014, Adams 2016). It is expected that the urbanized area will double in its size and host around 5 billion people by the year 2030 (Sukopp 1998, Seto et al. 2012, UNPD 2014). Likewise, also the economic growth and demographic changes that accompany this "urban sprawl" will increase (Alberti et al. 2003, Grimm et al. 2008, Pickett et al. 2008). Urbanization destroys natural landscapes and creates highly fragmented habitats through the spread of artificial structures (Baker & Harris 2007, Ramalho & Hobbs 2012, McCleery et al. 2014). This negatively affects the distribution patterns of some species (McKinney & Lockwood 1999; McKinney 2002, 2008), but increases the abundance of others which can lead to human-wildlife conflicts in some cities (red foxes, *Vulpes vulpes*: Gloor et al. 2001, Wandeler et al. 2003; European badgers, *Meles meles*: Harris 1982, 1984 or raccoons, *Procyon lotor*: Prange et al. 2003, Gehrt 2004). As natural environments are becoming less available it is not surprising that an increasing body of urban ecological studies has shown that during the past five decades, cities provide new habitats for a variety of plant and animal species (reviewed in Sukopp 1998, Wu 2014, McHale et al. 2015). Most recently, this is even the case for species that were previously assumed to be absent from cities (Rebele 1994, Meffert & Dziock 2012, Rodewald & Gehrt 2014). The research field of "biological patterns and associated environmental processes in urban areas" – as urban ecology is defined by Endlicher et al. (2007) – became highly interesting (Shulenberger et al. 2008; Wu 2008, 2014; Pickett et al. 2011) and also pressing from a conservation-oriented point of view (Dearborn & Kark 2010, Goddard et al. 2010, Adams 2014).

Species that initially have evolved under natural conditions with respective selection factors now live in areas of high anthropogenic influences; within the urban area, air temperatures up to 5 °C higher compared to the rural outskirt are caused by infrastructures like streets and buildings that highly store thermal energy ("urban heat islands, UHI"; OKE 1982, MCDONNELL ET AL. 1993, GRIMM ET AL. 2008). Although precipitation is usually increased in cities due to the high amount of aerosols that facilitate cloud formation (SHEPHERD ET AL. 2010) water is mostly directly drained off the land (GRIMM ET AL. 2008, PICKETT ET AL. 2008) and a rather dry and warm microclimate prevails. This urban-specific microclimate supports longer vegetation and reproduction periods (KLAUSNITZER 1989, PARTECKE ET AL. 2004, DITCHKOFF ET AL. 2006) and in turn, leads to a higher and more consistent availability of food throughout the year. This not only increase longevity (e. g., in raccoons: PRANGE ET AL. 2003 or fox squirrels, *Sciurus niger*: MCCLEERY ET AL. 2008) but also reduces migratory behavior (in birds: JOKIMÄKI & SUHONEN 1998, KARK ET AL. 2007, MØLLER 2008). Along with reduced predation pressure and spatial limitation of suitable habitat due to fragmentation, wildlife densities increase and individual territory sizes are often reduced for urban populations compared to rural ones. This has been shown for several bird species (MARZLUFF ET AL. 2001, MØLLER 2009), the red fox (ADKINS & STOTT 1998) and the European badger (DAVISON ET AL. 2009). Shifts in activity patterns induced by anthropogenic disturbance (RILEY ET AL. 2003, KARK ET AL. 2007), in communication behavior caused by urban noise background (SLABBEKOORN & PEET 2003, NEMETH & BRUMM 2009) or in diet and feeding habits in response to artificial food sources (HARRIS 1984, LEFEBVRE 1986) are also common adaptations of animals that live in cities. However, higher population densities within the urban landscape lead to a higher risk of disease transmission between individuals and increase intraspecific competition, e. g., for food or suitable breeding sites (reviewed by DITCHKOFF ET AL. 2006, RILEY ET AL. 2014). In turn, higher stress levels negatively affect physical conditions and eventually cause higher intrinsic mortality rates in urban populations (PARTECKE ET AL. 2006, STRASSER & HEATH 2013, RILEY ET AL. 2014). An increased risk of traffic accidents (in European rabbits: PLANILLO & MALO 2013) and an increased exposure to chemicals (in birds: GETZ ET AL. 1977 and red foxes: DIP ET AL. 2003) further negatively influence survival rates of urban and suburban wildlife populations (see also FORMAN & ALEXANDER 1998, ETTER ET AL. 2002, RILEY ET AL. 2014).

It is now the great challenge of urban and evolutionary ecologists worldwide to discover factors that are involved in the adaptation of a species to human-induced land changes and to reveal whether changes in life history, behavior and physiology are the results of phenotypic plasticity or genetic adaptations (DITCHKOFF ET AL. 2006, PARTECKE ET AL. 2006, RAMALHO & HOBBS 2012).

The aim of my doctoral thesis was to investigate effects of gradual anthropogenic habitat alteration on the ecology and behavior of European rabbits (*Oryctolagus cuniculus*, L., 1758) in and around Frankfurt am Main, Germany. In rural areas all throughout Europe, the European rabbit faces severe declines and is categorized as "near-threatened" by the IUCN in its original distribution area on the Iberian Peninsula (Smith & Boyer 2008). Aside of the spread of introduced diseases such as Myxomatosis since the 1950s (in Great Britain: Armour & Thompson 1955), and Rabbit Hemorrhagic Disease (RHD) in the late 1980s (in Spain: Villafuerte et al. 1995), especially intensified agricultural practices and altered forms of land use (Moreno & Villafuerte 1995, Delibes-Mateos et al. 2010) further caused population declines of this mammal within the last six decades (Moreno & Villafuerte 1995, Lees & Bell 2008, Ferreira et al. 2014). In addition, *O. cuniculus* is a common game species in Europe (Angulo & Villafuerte 2004, Ferreira et al. 2014) and hunting further reduced population densities. In Germany, hunting bags decreased dramatically over the last years in almost all rural areas whereas in cities like Berlin, Munich or Frankfurt densities were even increasing and populations regulated through hunting (Arnold et al. 2013).

The main focus of my thesis was to investigate whether urbanization is indeed a predictor for rabbit densities along the rural-to-urban gradient and if so, to reveal the causes of discrepancies between population dynamics in and around Frankfurt. In addition to (1) population dynamics (population densities and group sizes), I compared (2) habitat use (e. g., burrow distribution and external burrow construction features), (3) activity patterns (e. g., time spend on anti-predator behavior) and (4) the intraspecific communication behavior via latrines between populations. The lack of scientific research on the response of *O. cuniculus* to anthropogenic nuisance highly rendered the necessity of my research also from a conservation orientated perspective.

Chapter Overview

The following subchapters (of Chapter 1) provide the main results, conclusions and a critical discussion of each of the four above mentioned research topics. At the end of Chapter 1, I summarize the outcome of my studies from a broader scientific perspective and provide additional data on population genetics and home range sizes of the studied rabbit populations. Accordingly, in Chapter 2-5, the respective publications are attached, which have all been published in peer-reviewed scientific journals. Except the study that handles the effect of urbanization on rabbit population densities in Chapter 2 (national journal) all manuscripts are published in international scientific journals.

Quantifying the degree of urbanization and its effects on population densities of the European rabbit (Chapter 2).

The first studies within the field of urban ecology focused on the comparison of population densities of wildlife species between the urban matrix and the rural outskirts (Marzluff et al. 2001, Magle et al. 2012, Rodewald & Gehrt 2014). Obviously, organisms can only establish populations in cities successfully when they are able to adjust to the urban-specific abiotic and biotic conditions, e. g., the altered microclimate (McKinney 2002, Kowarik 2011, Adams 2016) or the permanent human presence (Partecke et al. 2006, Evans et al. 2010, Adams 2016).

Base on differences in population densities, urban ecologists suggest to classify species into "urban dependents", "urban exploiters", "urban tolerants", "urban avoiders" and "urban impossibles" (reviewed in Rodewald & Gehrt 2014). Typical urban dependents are the house mouse, *Mus musculus*; the rock pigeon, *Columba livia* and the house sparrow, *Passer domesticus* (Kark et al. 2007, Rodewald & Gehrt 2014, see also McKinney 2002). These species usually reach highest abundances in the city center whereas in suburban and rural areas their densities decrease (Rodewald & Gehrt 2014). Being rather small and mobile urban dependents are able to use anthropogenic resources even in areas of highest human disturbances (Shochat 2004, Magle et al. 2009). In contrast, urban exploiters like red foxes (Adkins & Stott 1998, Wandeler et al. 2003), badgers (Davison et al. 2008, 2009) or squirrels (Chapman et al. 2012) reach maximum densities in larger green fragments or park areas located within the urban and suburban matrix. Rural populations of urban exploiters often occur under highly heterogeneous habitat conditions where different landscapes alter on small local scales (Shulenberger et al. 2008, Tuomainen & Candolin 2011, Ryan & Partan 2014). These so called "edge habitats" are typical for modern cities too as here, various forms of land-use create mosaics of gardens, parks, waste lands etc. Hence, animals that are able to tolerate a wide range of ecological conditions are favored to permanently occur within urban areas (McKinney 2002, 2006; Sih et al. 2011). Having in common a high fecundity, urban exploiters can reach high population densities within short time periods and often cause human-wildlife conflicts (Gehrt 2004, Duduś et al. 2014, Adams 2016). The behavioral flexibility of raccoons, for example, allows them to use anthropogenic food sources and shelter-providing structures in close human proximity without depending on them (Harris 1984; see also Tuomainen & Candolin 2011). Likewise, densities of this mammal have been observed to be five times higher in cities in comparison to rural environments (Hadidian & Smith 2001, Prange et al. 2003).

Urban tolerants like bobcats, *Lynx rufus* or white-tailed deer, *Odocoileus virginianus* only occasionally use anthropogenic resources that are located within suburban and urban areas (George & Crooks 2006, Rodewald & Gehrt 2014). In some cases, densities of these species can be increased locally in cities but, such populations are usually characterized by high mortality and low reproduction rates (observed in several reptiles, amphibians and bat species; reviewed in Rodewald & Gehrt 2014). Urban avoiders as Mountain lions, *Puma concolor* (Iossa et al. 2010); gray wolfs, *Canis lupus* (Rodewald & Gehrt 2014) and some migratory bird species (Rodewald & Bakermans 2006) have been observed as single (transient) individuals in cities but seem to be unable to establish populations within the urban and suburban environment. Finally, urban impossibles are clearly absent from urban areas, e. g., snow leopards, *Panthera uncia* or spotted owls, *Strix occidentalis* (Alberti et al. 2001, Rodewald & Gehrt 2014). Both, urban avoiders and urban impossibles have highly specific habitat demands and are very sensitive to human-induced disturbances. As a result, these species are extremely threatened by the process of urbanization.

The suggested classifications into urban dependents, urban exploiters etc. need to be considered with caution and should only give a vague understanding of how certain species respond to the process of urbanization. For example, high population densities in American cities suggest the coyote, *Canis latrans* to be an urban exploiter but, at the same time, urban populations of this mammal show many characteristics that are rather typical for urban avoiders (McClennen et al. 2001, George & Crooks 2006, Gehrt 2007). Gehrt (2007) found that urban coyotes avoid human presence by changing their activity patterns and not using anthropogenic food sources. Clearly, habitat-specific factors of a city and the species-specific ecology always play an important role causing high population densities and typical behavioral adaptations of a certain species in one city, but the absence of the same species in another (Sih et al. 2010, 2011; reviewed in Magle et al. 2012, Rodewald & Gehrt 2014).

Only few of the yet available studies include a measurement of the intensity of wildlife exposure to urbanization. Instead, a subjective classification into "urban", "rural" and sometimes "suburban" or "peri-urban" sites has been used to merely assumes a linear gradient from the city center towards the rural outskirt (Sukopp 1998, Endlicher et al. 2007, MacGregor-Fors 2011). Nevertheless, especially newly planned sites within cities still comprise remnants of natural landscapes causing the urban matrix to become a polycentric entity where land cover does not necessarily follow anymore this "classical" rural-to-urban gradient (McDonnell & Hahs 2008, McKinney 2008, Qureshi et al. 2014). Consequently, the consideration of several variables that are suitable to reflect local variations in the intensity of urbanization, like the percentage of sealed surface or the intensity of human disturbance has been emphasized by several leading ecologists (McDonnell & Pickett 1990, Blair 1999, Zipperer et al. 2000). Although the common use of such variables would facilitate the comparison of studies from different cities, no such approach gained acceptance by today (Loucks 1994, Wu 2014).

In my first study presented in Chapter 2, I asked whether the degree of urbanization is indeed a predictor for differences in European rabbit densities in Frankfurt and its hinterland. Here, rabbit populations occur in small green spaces within the inner city center, in most of the parks located at the former periphery of the administrative district and in some adjacent rural areas (see Ziege et al. 2015, page 56 and Ziege et al. 2016b, page 79). To quantify local variations in the degree of urbanization within the total of 17 different study sites I decided to consider two variables of demographical nature (intensity of human disturbance and population densities of human residents) and two variables of physical nature (proportion of artificial ground cover and numbers of anthropogenic objects) in summer 2011. According to literature these variables are frequently used when it comes to the definition of a "city" (McKinney 2002, McDonnell & Hahs 2008, MacGregor-Fors 2011). Through transect counts the intensity of human disturbance (including leashed and unleashed dogs) per min and ha was recorded during the main activity period of the rabbits at dawn and dusk. Population densities of residents within a radius of 500 m from the edge of each study area were obtained from the registration office (*Einwohnermeldeamt*) of Frankfurt. The proportion of artificial ground cover (e. g., streets, play grounds etc.) and numbers of anthropogenic objects per ha within the study areas were determined using ArcGIS 10 and map material provided by the land surveying office (*Stadtvermessungsamt*) of the city of Frankfurt. The data of all four variables were log-transformed and subjected to a principal component analysis (PCA) that led to one continuous variable, henceforth referred to as the "degree of urbanity".

Regarding the comparison of rabbit population densities between different habitat types that differ in the probability of animal sightings, several direct and indirect methods have been evaluated (Palomares 2001, Moreno et al. 2008, Barrio et al. 2010). I decided to use two direct approaches by determining numbers of rabbit individuals per ha through census counts and direct observations at the burrows and one indirect method through the assessment of burrow densities. Census counts have been performed along pre-defined transects during dusk and dawn on three consecutive days in the end of September and beginning of October 2011, when rabbit density was most likely to reach its peak at the end of the reproduction period (Sneddon 1991, von Holst et al. 2002).

In order to calculate numbers of burrows per ha I had to distinguish separate rabbit burrow systems from each other. From October till March, local hunters use a hunting regime that is only successful when all entrances belonging to the same burrow are sealed with cages (hunting licence ID 1000250221). The hunters release ferrets, *Mustela putorius furo* into the burrow to chase rabbits out, which then get trapped in cages ("ferreting", Figure 1.1). I took advantage of this approach for almost all burrow systems that were previously mapped by walking transects within the different study sites. Where this method was not applicable (e. g., due to restrictions in hunting law) I relied on a different indicator that allows to identify separate burrows from each other. Out of his long-term experience, one hunter has observed that the funnels of entrances belonging to one burrow system almost always point towards a common center. This center was also defined as the "center point" of the burrow systems from which I took GPS coordinates.

Figure 1.1: (a) Ferret (*Mustela putorius furo*) at rabbit burrow entrance. (b) Cages used for "ferreting". (c) Rabbit trapped in cage. Photos: A. Seidemann

While estimating rabbit and burrow densities I also assessed flight initiation distances (FIDs) as another common and easy measurable indicator to account for behavioral adaptations in response to human disturbance (Tarlow & Blumstein 2007, Møller 2008, McCleery 2009). The FID is defined as the distance to which a human can approach before an animal starts altering its behavior as a clear sign of disturbance (Tarlow & Blumstein 2007). Using non-parametric Spearman rank correlations number of rabbits and burrows per ha as well as the FIDs were correlated with the continuous variable "degree of urbanity". All statistical analyses were conducted in SPSS version 13.0 for windows. I expected to find a positive correlation between number of rabbits and burrows per ha and the degree of urbanity. Moreover, I proposed the shortest FIDs in populations located within sites of highest degree of urbanization in Frankfurt as a behavioral adaptation to human nuisance. This is exactly what my study revealed: rabbit and burrow densities increased with increasing degree of urbanity while FIDs decreased and were shortest for rabbit populations located within the city center of Frankfurt (see Ziege et al. 2013; pages 44,45).

When considering the ecology of the European rabbit it becomes clear why this mammal is able to establish high population densities within large cities like Frankfurt. Lombardi et al. (2007) showed that the availability of suitable sites for breeding (burrow construction sites in thick vegetation) positively affects the reproduction rate of *O. cuniculus*. In rural areas where land-use diversity is still high, e. g., fields, thickets, open grasslands or gardens alternate, rabbits reach highest densities (Lombardi et al. 2003, Calvete et al. 2004, Guerrero-Casado et al. 2013). Here, the mosaic-like landscape structures provide access to shelter and food in close proximity and thus, meet the animals' habitat requirements best (see also the concept of "edge species", Ryan & Partan 2014). However, as a result of the ever ongoing increase of the human world population, the demand of highly productive agricultural areas increases constantly (Pickett et al. 2008, Edmondson et al. 2011). This, in turn, leads to intensively used rural areas where homogenous, open landscape patterns dominate and thickets for burrow constructions are scarce (McKinney 2002, Delaney et al. 2010, Edmondson et al. 2011). I argue that differences in habitat quality were the major reasons for the shifts in rabbit and burrow densities between the 17 study sites. The four study sites with the lowest degree of urbanization were mostly rural, agriculturally used areas where large rape and wheat fields and high-grass orchard meadows dominated. Between meadows and fields, only a few patches of thickets (mainly blackberry bushes) were suitable sites for the construction of burrows. In contrast, the habitat pattern of the urban and suburban study sites was more heterogenic, with parks, gardens and green spaces altering on a small scale, not only increasing the access to shelter-providing structures, but also to food including human waste and deliberate feeding (see also Niemelä 1999, Kowarik 2011, Zhang et al. 2013). Accordingly, rabbit densities were highest at these urban study sites.

Rodewald and Gehrt (2014) reviewed density-dependent and density-independent factors that influence population dynamics of wildlife within urban habitats. For example, a milder microclimate, higher resource availability, and a mostly reduced predation and hunting regime are factors that buffer negative population dynamics within cities (but see Fleischer et al. 2003 and Aldredge et al. 2012 for contradicting studies on Florida scrub-jays, *Aphelocoma coerulescens*). Concerning my study, I argue that stronger weather fluctuations at rural areas were likely to directly increase mortality rates of *O. cuniculus* (especially of young individuals) during cold and wet winter times, and indirectly through a less predictable food availability (Rödel et al. 2004, Rödel & Dekker 2012). In contrast, within cities the warmer microclimate not only increases the probability of winter survival but might as well cause rabbits to start earlier with reproduction. In the city center of Frankfurt young rabbits were indeed visible earlier in the year in comparison to rural study sites. These observations were in line with a study of Schieber (1983) who reported rabbits in the city of Munich to start breeding earlier compared to their rural conspecifics. In addition, I found evidence that rabbits in the city had better access to food sources during winter time, e. g., I frequently observed humans that intentionally fed rabbits.

Differences in predation pressure is another aspect that explains differences in population densities as well as FIDs along the examined rural-to-urban gradient (Shochat 2004, Fischer et al. 2012, Uchida et al. 2015). In general, top predators are absent in cities but as mentioned above, medium-sized predators ("mesopredators") as badgers, foxes or raccoons can reach high densities (Prange & Gehrt 2004, Prugh et al. 2009, Fischer et al. 2012). Aside of the red fox other common natural predators of the rabbit are mustelids or birds of prey (Sneddon 1991, von Holst et al. 2002). Duduś et al. (2014) reported high abundances of stone martens, *Martes foina* or tree martens, *Martes martes* within urban environments. Also kestrels, *Falco tinnunculus* (Kübler et al. 2005); northern goshawks, *Accipiter gentilis* (Rutz 2006) or sparrow hawks, *Accipiter nisus* (Risch et al. 1996) are reported to reach high abundances within the urban landscape. Moreover, free-ranging domesticated dogs and cats might play a role as non-natural predators and eventually caused high death rates to juveniles (von Holst et al. 2002, Lepczyk et al. 2004). However, accounting for the mere presence of rabbit predators does not necessarily translate into the actual predation pressure they exert on their prey. For example, 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 (McClennen et al. 2001, Riley et al. 2003, Ditchkoff et al. 2006). Additionally, it has been proven for red foxes (Contesse et al. 2004) or Cooper's hawk, *Accipiter cooperii* (Estes & Mannan 2003) that these species start using other (more abundant) food sources.

I noted any predation attempt by natural and non-natural predators, but only occasionally observed free-ranging dogs and cats that chased rabbits into their burrow systems. I also found rabbit carcasses on streets but, as only in a few cases I was able to doubtlessly identify traffic accidents as the cause of death, I did not further quantify these numbers. To gain a realistic impression on mortality rates of rabbits it would have been necessary to observe animals for 24 hours over the course of several days. Although I was not able to realize this approach I still argue that an overall lower predation risk additionally promotes high population densities and shorter FIDs of *O. cuniculus* populations within the city. The latter allows for coexistence with humans without behavioral disruption, leading to lower energy expenditure, and thus reduced stress responses (Ditchkoff et al. 2006, Møller 2008, but see also French et al. 2008).

Effects of urbanization on burrow characteristics and group sizes (Chapter 3).

Some bird species (Luniak 2004, Burger & Gochfeld 2009) and mustelids (Herr et al. 2010) use the increased variety of nest sites provided by the high portion of buildings in cities whereas other species rather establish den sites beneath unoccupied buildings or in areas of restricted public access (red foxes in Toronto, Canada: Adkins & Stott 1998 or Melbourne, Australia: Marks & Bloomfield 2006). The stone marten is even known to shift its denning behavior due to seasonal temperature variations, using nest sites with poor thermal isolations in summer, e. g., uninhabited buildings, but prefer inhabited buildings during the coldest months of the year (Herr et al. 2010). In contrast, stone martens at rural areas use natural structures for denning purposes (Herr et al. 2010).

To date, only one study exists that compares differences in the distribution pattern and the external construction features of mammalian burrows at rural and urban sites. Davison et al. (2008) found the main burrows of urban badger populations in Brighton, southern UK to have significantly fewer entrance holes compared to those located at rural areas. Aside of the fact that urban badgers may have recently migrated into cities and thus, had not the time yet to enlarge their burrow systems to a size comparable to those of their rural conspecifics, shifts in the social badger organization are likely to play another important role. Davison et al. (2008) observed urban badger populations to be less cohesive mainly due to a better access to food sources. The authors suggested that urban badgers form smaller social groups, which, in turn, leads to burrows with fewer entrances.

Lombardi et al. (2003, 2007) compared rabbit burrow characteristics in three rural habitats on the Iberian Peninsula that differed in the availability of sites suitable for burrow constructions (dense bushes, thickets etc.) and food, but were similar in terms of predation pressure. Within the ecotone habitat, where food and cover were available in close proximity to each other, rabbit and burrow densities were highest (LOMBARDI ET AL. 2003). In the scrubland, food was limited but the high availability of bushes translated into a more uniform/random burrow distribution pattern. In contrast, within the grassland habitat, where dense cover was the limiting resource, burrows were confined to few sites, which led to an aggregated burrow distribution pattern. Moreover, in the grassland habitat burrows were larger compared to the ones in the ecotone and scrubland, had higher numbers of entrances and were hosted by larger rabbit groups. Other studies further approved the relation between habitat quality, number of burrow entrances and group sizes: At sites where resources were not limited burrow density was higher but number of entrances was comparably low as well as the number of rabbits that occupied these burrows (MYERS & POOLE 1959, COWAN 1987). The aim of the study presented in Chapter 3 (ZIEGE ET AL. 2015) was to clarify the suggested role of habitat quality between the different study sites, e. g., the availability of suitable sites for burrow construction. In addition, I compared the external burrow construction behavior of the rabbit populations and addressed group sizes as another aspect that is known to be influenced by the actual predation risk within an area.

In line with my argumentation that heterogeneous landscape patterns within urban and suburban areas offer a variety of suitable sites for burrow construction, e. g., within (thick) bushes in gardens and parks, I proposed the following hypotheses for my second study: With increasing degree of urbanity rabbit burrows become more uniformly distributed while the number of burrow entrances as well as the number of rabbits that occupy the same burrow decreases. According to the *Stadtarchiv Frankfurt am Main*, rabbit populations are established in the city district of Frankfurt since at least 1930. Thus, potential differences in size and complexity of burrow structures between the study sites are unlikely to be caused by differences in time spans of burrow establishment as suggested by DAVISON ET AL. (2008). I rather argue that habitat fragmentation within highly urbanized areas limits the external expansion of burrows. Furthermore, as large burrows with many entrances provide better protection from predators (rabbits: COWAN 1984; voles: HARPER & BATZLI 1996) a reduced predation pressure within urban and suburban sites should further favor small burrow systems hosting small rabbit groups.

Based on the GPS locations of all burrows mapped within the study sites, I used two different approaches to identify whether burrows are aggregated, randomly or uniformly distributed. Adopted from LOMBARDI ET AL. (2003), I calculated the Index of dispersion (ID) which is the observed variance divided by the mean number of burrows in 50 x 50 m quadrants within each study site (see also KREBS 1999). ID values close to 0 indicate a uniform distribution, whereas values much larger than 1 indicate an aggregated distribution pattern (Krebs 1999). The second, more fine-scaled method refrained from assigning burrows to distinct quadrants within the study area but considered the distances between each burrow and its nearest neighbor (see Gea-Izquierdo et al. 2005). These distances have been used to calculate the Index of aggregation (RD, Donnelly modification) where RD values approach 0 if spatial burrow patterns are aggregated (Krebs 1999).

To accurately assess the number of burrow entrances and the group size for all study sites (except the rural area "Götzenhain" due to hunting law restrictions), I took again advantage of the yearly local hunting regime in autumn 2012. Additionally, a total of 19 urban, 20 suburban and 19 rural burrows were randomly selected for an in-depth analysis of external burrow structures (Kolb 1985). In this case, study sites were categorized as rural if their "degree of urbanity" was $\leq$ -0.5, as suburban with values > -0.5 and $\leq$ 0.5 and as urban with values > 0.5. The mean distances between all burrow entrances and the height and width of each entrance (area of the main hole leading into soil) and inlet (area of the funnel in front of the hole shaped by rabbits while entering and leaving the burrow) was measured. All variables were correlated with the degree of urbanity using several Spearman rank correlations with respective Bonferroni correction of significance levels to avoid alpha-error inflation.

The results of this second research project further confirmed the conclusions I drew from the first study on population dynamics: As expected, with increasing degree of urbanity burrows became more uniformly distributed while the number of burrow entrances decreased and likewise the number of rabbits that occupied one burrow (Ziege et al. 2015; pages 57,58). Moreover, the external dimensions of the burrows were negatively related with the degree of urbanity, i. e., distances between burrow entrances were shortest within the city center. Interestingly, the mean width of burrow entrances was comparable for burrows located within rural and suburban study sites, but was significantly narrower for burrows at urban study sites (Ziege et al. 2015, page 58).

Apparently, mosaic-like habitat structures in the city district of Frankfurt offers *O. cuniculus* populations a variety of suitable sites for burrow construction which is reflected by a uniform/random burrow distribution pattern (Figure 1.2.). At the same time artificial structures as streets and pathways limit the external expansion of burrow systems within highly urbanized areas. Additionally, I found rabbits' burrows to be destroyed over time by private land owners or as part of urban management strategies when established close to roads, buildings or private gardens. Therefore, the rabbit seems to be another example of a species that causes human-wildlife conflicts within cities leading to respective management actions (see also Davison et al. 2008 for urban badger populations in the UK, reviewed in Adams 2016).

Figure 1.2: (a) Rural study site "Kriftel". (b) Suburban study site "Rebstockpark". (c) Urban study site "Taunusanlage". White triangles indicate rabbit burrows. Source: Google Earth

Another possibility is that differences in soil conditions cause the shifts in complexity of burrow systems. Cowan (1987) and Gea-Izquierdo et al. (2005) for example, reported smaller rabbit burrows in areas with loose, sandy soils. Although I did not assess soil characteristics at my study sites, I believe that this aspect plays a negligible role compared to population densities, resource availability and predation risk. Despite the overall trend of burrow systems to become smaller with increasing degree of urbanity, I also located some small burrows at the rural study sites and some complex and large burrow systems at highly urbanized areas.

In Ziege et al. (2013), I pointed out that the negative relation between FIDs and the degree of urbanity is likely to be caused by changes in predator-prey-interactions between study sites. Hence, due to the diminished predation risk by avian and terrestrial predators in urban areas, city rabbits might not benefit from investing in the construction of larger and thus safer burrows, i. e., with more entrances (Cowan 1984). Variations in the height and width of entrances between urban and rural/suburban burrows are as well likely to be caused by differences in predation pressure and respective variations in utilization frequencies. Especially at urban study sites, fewer rabbits enter and leave their sheltering burrows less often and also at a reduced speed compared to rural sites. In addition, the necessity to face the costs of living in large groups for a better protection from predation is reduced within urban and suburban populations. This is also true when considering the formation of large groups due to thermal advantages. It has been shown in sugar gliders, *Petaurus breviceps* (Fleming 1980) and alpine marmots, *Marmota marmota* (Arnold 1988) that the per capita thermal energy loss within large groups is smaller. As temperatures in cities are generally higher (Pickett et al. 2011), the necessity for urban rabbits to live in large groups is reduced compared to rural populations. Whether living in the city *per se* led to smaller group sizes, e. g., due to relaxed predation pressure and milder temperatures, and if burrow structures changed as a consequence of this, or *vice versa* could not be revealed.

Effects of urbanization on activity patterns and time budgets (Chapter 4).

Aside of measuring FIDs the percentage of the time an animal spend on anti-predator behavior, e. g., screening the environment for predators or concealing themselves underground is an indirect measurement for the predation pressure that exists in a habitat (Brown et al. 1999, Carrete & Tella 2009, Chapman et al. 2012). Just as the available studies on shifts in predation regimes within the urban and suburban landscape often have contradicting outcomes – underlining the practical difficulties to gain reliable field data – studies on activity patterns and time budgets of different species likewise yielded contradicting results. Where some animals in the urban habitat performed more anti-predator behaviors compared to their rural conspecifics (in woodchucks, *Marmota monax*: LEHRER ET AL. 2011) it was the opposite in other species (in cape ground squirrels, *Xerus inauris*: CHAPMAN ET AL. 2012; see also the "risk-disturbance hypothesis": FRID & DILL 2002, MAGLE & ANGELONI 2011).

The European rabbit is known to adapt behaviorally to different habitat types characterized by varying predation risk and availability of resources like refuge and food (LOMBARDI ET AL. 2003, 2007). However, previous studies only considered rural rabbit populations, while comparisons of populations exposed to different levels of urbanization are as yet lacking. In ZIEGE ET AL. (2016a) presented in Chapter 4, I compared the time animals spent outside their burrows as well as the time that was invested in different behaviors when being above ground. From one hour before sunrise until one hour after sunset the number of rabbits was noted every 15 min that were visible within a radius of 50 m around the focal burrow at three different burrows located in the city center of Frankfurt (urban), four burrows at suburban sites Rebstockpark and Ostpark, as well as three burrows in the adjacent rural areas Bad Vilbel and Maintal (see ZIEGE ET AL. 2016a, page 67). In order to quantify the intensity of human disturbance, the number of pedestrians and dogs (leashed and unleashed) within this 50 m radius was counted. In between these scans, an adult focal animal was randomly selected and its behavior recorded for 15 min or until it moved out of sight. In accordance to GIBB (1993) and MAGLE AND ANGELONI (2011), the duration of anti-predator behavior such as vigilance (lifting head, ears straight, standing on the hindfeet) and flight behavior (fast movement caused by disturbance) as well as behavioral categories as digging, grazing, self-grooming, moving (where individuals slowly change their position but do not flee from disturbance), resting, and social interactions (amicable: mutual grooming, playing, nose-to-nose contact; agonistic: biting, fighting, chasing) was recorded. I presumed that due to relaxed predation pressure, urban rabbits spend more time outside their protective burrows during the day compared to rural individuals. In addition, when outside of their burrows, rabbits located within the urban matrix should invest the least amount of time in an anti-predator behavior as a behavioral adaptation in response to the permanent human presence.

ADAMS ET AL. (1987) reported that urban black-tailed prairie dogs, *Cynomys ludovicianus* conceal themselves considerably shorter in their burrow systems after a human-induced predator attack compared to rural conspecifics. Derived from this study, I also conducted such a concealment experiment for 15 different rural, suburban and urban rabbit groups each. Animals were urged to enter their respective burrow by a human approach and from a hidden observation spot, the time was recorded until animals reappeared above ground ("concealment time"). The experiment was terminated when the observer was not able to force the rabbits underground. This was the case at almost all urban burrows, which had to be excluded from the analysis. To investigate whether frequent human disturbance leads to a reduction of the time rabbits spend engaging in anti-predator behaviors (i. e., shorter concealment times), the simulated predator attack was repeated five times at five randomly selected rural and suburban burrow systems. I expected suburban rabbits to habituate faster to the repetitive simulated predator attacks, i. e., animals spend less time in their burrows.

All relative data were arc-sine square root transformed to meet the prerequisites of statistical tests that base on the standard normal distribution. The "percentage of rabbits above ground" was used as the dependent variable in a linear mixed model (LMM). The 15 min observation period was nested within "burrow ID" and used as a random factor. The variables "urbanity", "time passed since sunrise", and "intensity of disturbance at burrow" for each burrow and focal scan were explaining variables. The gradient analysis was not applied in this study because of the relatively low number of different study sites. By using pairwise Spearman rank correlations with Bonferroni corrections, I compared the mean values for each behavioral category (anti-predator behavior etc.) between urban, suburban and rural groups. Concealment times were analyzed with a non-parametric Mann-Whitney U-test and a repeated measures general linear model (rmGLM).

As hypothesized, in contrast to rabbits at rural study sites, I found rabbits at urban and suburban sites to spend on average more time outside their burrows even showing a less pronounced daytime rhythmicity including a weaker midday resting phase. I further discovered – as expected – that rabbits at urban and suburban study sites invested less time in anti-predator behavior. Thereby, suburban individuals that spent lowest proportions of time on anti-predator behaviors over the course of the day invested more time into grazing and resting compared to their urban and rural conspecifics (ZIEGE ET AL. 2016a; pages 69,70). This is in line with the study of CHAPMAN ET AL. (2012) who found "peri-urban" populations of cape ground squirrels to spent most of their time in grazing behavior during summer when being above ground in comparison to rural and urban populations. 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 then their urban conspecifics. No evidence suggested that access to food resources at the suburban sites of my study was low. With repeated sampling, concealment times decreased over time but, I was not able to detect differences between suburban and rural rabbit groups (ZIEGE ET AL. 2016a, page 69).

The main conclusion of this study was that rabbit populations from urban and suburban study sites are well habituated to anthropogenic disturbance and are likely exposed to a lower risk of predation by avian and terrestrial predators as it is the case for rural sites. Apparently, the suburban habitat offers the least stressful conditions for rabbits as here, not only the predation pressure by natural predators seems to be lower in comparison to rural sites (Fischer et al. 2012, Ryan & Partan 2014; see Blair & Johnson 2008 for bird species). Also, the human disturbance factor was less intense then what was measured within urban sites and rather comparable to rural sites (Ziege et al. 2016a, page 69). This observation explains why I found no differences in the concealment time between suburban and rural groups.

My argumentation finds further support by the fact that urban rabbits invested considerably more time into above ground moving then suburban and rural individuals. I considered this steady "above-ground-movement" of urban rabbits as a "low-cost" strategy to avoid disturbance by elude a human's approach. This assumption is also confirmed by the fact that in 97 % of all cases, I was not able to induce urban rabbits to enter their protective burrow during the concealment experiment.

Effects of urbanization on communication behaviors (latrine-based marking networks) (Chapter 5).

In the communication system of many mammals, the exchange of information about an individual's age, sex, reproductive condition, and social status are often based on olfactory signals transmitted through feces and urine in localized defecation sites, so called "latrines" (Figure 1.3) (Kruuk 1995, Stewart et al. 2001, Ralls & Smith 2004). Comparable to the latrine marking behavior of badgers (Kruuk 1978, Roper et al. 1993), gazelles (Wronski & Plath 2010, Wronski et al. 2013) or primates (Irwin et al. 2004, Dröscher & Kappeler 2014), *O. cuniculus* either establish latrines in central areas within their home range to facilitate within-group communication (core marking) (Mykytowycz & Hesterman 1970, Hesterman & Mykytowycz 1982) or at territorial boundaries for between-group communication (peripheral marking) (Mykytowycz & Gambale 1969, Mykytowycz et al. 1976). Core marking is suggested to support the monopolization of key resources by individuals (food, burrows, or nesting sites) and the maintenance of social structures within the same group whereas peripheral latrines serve as a visual and olfactory fence towards neighboring (male) territory holders (Mykytowycz & Gambale 1969, Wronski et al. 2006, Jordan et al. 2007). Hence, it is well conceivable that the relative importance of both marking behaviors (core vs. peripheral) highly depends on population densities and group sizes (reviewed in Dröscher & Kappeler 2014).

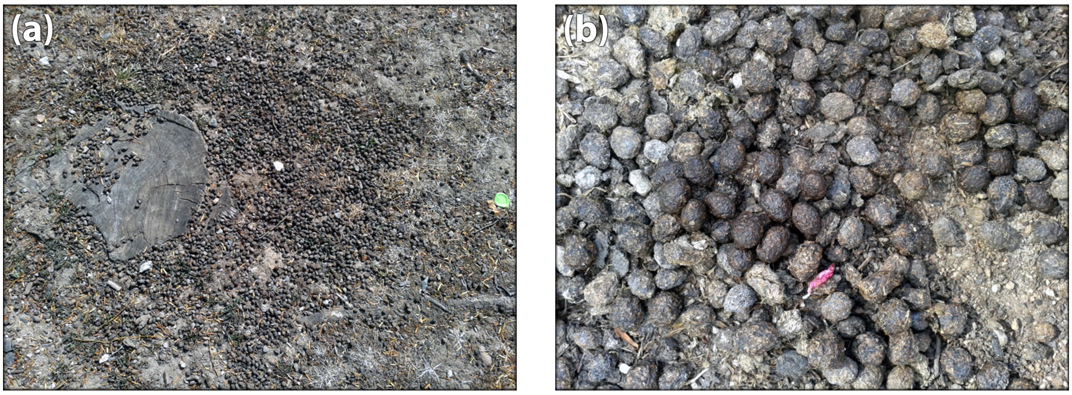

Figure 1.3: (a) Latrine of *O. cuniculus*. (b) Fresh fecal pellets on latrine. Photos: M. Ziege

Studies on rural *O. cuniculus* populations suggest that also predation pressure influences the latrine marking behavior. Latrines are mainly placed on bare soil, clearings, or elevated areas (e. g., on anthropogenic objects) and close to bushes, trees or other sheltering structures (Sneddon 1991, Monclús & de Miguel 2003). This trade off between visibility and accessibility reduces the risk of falling victim to avian and terrestrial predators while animals visit latrines. Indeed, in areas where predation pressure is high rabbits rather use latrines close to the protective burrow compared to peripheral, less save latrines (Monclús & de Miguel 2003, Domínguez-Cebrían & de Miguel 2013). Compared to studies on population dynamics and behavioral aspects as habitat use and anti-predator behavior, almost no investigations on adaptations in the social behavior of urban wildlife populations are available (Magle & Angeloni 2011, Magle et al. 2012, Rodewald & Gehrt 2014). Ziege et al. (2016b) presented in Chapter 5 is the first publication that ever compared the mammalian latrine-marking behavior within populations exposed to different intensities of urbanization.

In 2011, during the reproductive season from March to September, when territorial defense is strongest (Mykytowycz 1962, Sneddon 1991), I mapped latrines within two rural, four suburban and nine urban study areas. Latrines were defined as an accumulation of at least 20 single fecal pellets within an area of 20 x 30 cm (Virgós et al. 2003). For every latrine, its size and number of fecal pellets as indicators for long-term use was assessed, and number of fresh fecal pellets as an indicator for recent use was counted. Additionally, it was noted whether paw-scrapings as a clear sign for male territorial marking behavior were present at latrines (Bell 1977, Eisermann 1992). As the availability of thick vegetation is known to affect the placement and utilization frequency of latrines in rabbits (Monclús & de Miguel 2003, Domínguez-Cebrían & de Miguel 2013), the distance of each latrine to the next woody vegetation was measured as well. Finally, I calculated the mean distance of each latrine to its two nearest neighbors as an expression of latrine densities.

I related all variables to the distance of each latrine to the nearest rabbit burrow and applied several LMMs using the "degree of urbanity" as the explaining variable. Where core marking prevails, e. g., at study sites with large social rabbit groups, latrines close to the burrow should be used more often by the members of the same group than peripheral ones, which in turn should be reflected by higher numbers of (fresh) fecal pellets. In addition, overall latrine density ought to be higher close to the burrow in case of the prevalence of core marking. In accordance to my previous results, I expected latrine sizes, utilization frequencies, and latrine densities to increase with increasing distance to the burrow along the rural-to-urban gradient: High population densities at urban study sites increase competition for space, i. e., latrine marking at the periphery for territorial defense should be more important for urban rabbit populations (reported in badgers: HUTCHINGS ET AL. 2002, SCHLEY ET AL. 2004). In addition, in small rabbit groups that dominate at the city center of Frankfurt the necessity to communicate within the same group through extensive core marking should be less given. Here, also the use of peripheral latrines should be saver due to a reduced predation risk and a higher availability of shelter providing structures.

Latrine densities and utilization frequencies increased with increasing distance from the burrow along the rural-to-urban gradient, suggesting a higher importance of peripheral marking for rabbit populations located at highly urbanized areas. In contrast, not only was the proportion of latrines established in close proximity to the burrows highest at rural sites. Here, the inner latrines were also largest and contained more fecal pellets, suggesting that core marking prevailed (ZIEGE ET AL. 2016b; pages 82,83). The proportion of latrines at which paw-scrapings were present (a clear signal of male territorial behavior) was highest at urban study sites as well. This finding further supports my argumentation that strong intraspecific competition for resources at urban and suburban study sites increases the importance of male territorial demarcation at the periphery (ZIEGE ET AL. 2016b, page 84).

CRESSWELL AND HARRIS (1988) and DAVISON ET AL. (2009) accounted for the distribution of latrines in a low-density suburban European badger population in Bristol (UK) and a high-density urban population in Brighton (UK), respectively. Signs of peripheral latrine marking at territorial boundaries were neither found in the suburban Bristol population (CRESSWELL & HARRIS 1988) nor in the urban Brighton population (DAVISON ET AL. 2009) although this marking behavior is commonly observed in rural badger populations. DAVISON ET AL. (2009) suggested that even where relatively high population densities were reached territorial areas of distinct badger groups were not adjacent. Likewise, the need for territory demarcation through the deposition of latrines at territorial boundaries was less given compared to my study, where at urban and suburban study sites distinct social rabbit groups occupied territories in close proximity to each other.

Numbers of latrines decreased with increasing distance from the burrow system in rabbit population in a suburban forest of Madrid, Spain (Domínguez-Cebrían & de Miguel 2013). Authors discussed the prevalence of core marking in their population with high predation pressure however, no detailed information was provided (e. g., on population dynamics) that would have allowed conclusions regarding the question of how urbanization influence latrine-based communication behavior. In my study, relaxed predation pressure in urban sites and a higher availability of shelter-providing structures enabled the animals to also frequently use latrines at the periphery of their burrows compared to rural populations. At rural study sites, most latrines were found on meadows with short grass, especially close to pathways, while crop fields were largely avoided (see Ziege et al. 2016b, page 80). In the urban and suburban study area, landscape elements seemed not to have such a strong influence on latrine distribution patterns as meadows with short grass are common. Shorter distances between latrines and the nearest woody vegetation in urban areas were hence an additional indicator for my argumentation that urban landscapes offer a better access to dense vegetation compared to rural habitats (see Ziege et al. 2016b, page 84).

Another outcome of this research was the observation that with increasing degree of urbanity the proportion of latrines with fresh fecal pellets decreased. Aside of fewer group members that contribute to the establishment and maintenance of latrine-based communication networks in urban rabbit populations, in addition, also differences in climatic conditions between study sites might play an important role. As mentioned, higher ambient temperatures and altered patterns of precipitation are typical for urban areas and might accelerate the decay of fecal pellets. Moreover, a part of the fecal pellets is removed during the regular maintenance of green spaces, which, according to the *Grünflächenamt Frankfurt am Main*, is most intense in urban parks. Therefore, I suggest the number of (fresh) fecal pellets as a common measure for rabbit densities or for characterizing latrine-based communication networks should only be applied with caution in future comparative approaches (see also Villafuerte & Moreno 1997, Fernandez-de Simon et al. 2011, Kontsiotis et al. 2013).

Concluding remarks

The process of urbanization (“urban sprawl“) is considered to be one of the most extreme human-induced landscape alteration that leads to destruction of natural habitats and thus, loss of local and global biodiversity (Czech et al. 2000, Grimm et al. 2008, McDonald et al. 2008). With an ongoing growth of the human world population urban areas expand on a dramatic speed (Forman 2008, Dearborn & Kark 2010) and hence, the scientific research field of urban ecology has been paid increasing attention to during the last few decades (Sukopp 1998, Miller & Hobbs 2002). Aside of adaptation processes of wildlife in response to urban-specific habitat conditions, ecosystem services or human-wildlife conflicts are nowadays in the focus of urban ecologists (ALBERTI 2005, SHULENBERGER ET AL. 2008, WU 2014). Nevertheless, empirical data on the gradual influence of urban landscape features on the behavior, physiology and population genetics are not yet available for many species, however are a prerequisite for future conservation and management plans.

The four studies I presented in my doctoral thesis provided new insights into effects of human-induced habitat changes on wildlife concerning various ecological aspects. By inventing an approach that allowed me to include variations in the degree of urbanization within study sites I demonstrated for the first time that shifts in population dynamics of European rabbits along the rural-to-urban gradient are mainly driven by the availability of dense vegetation. Due to the behavioral flexibility of *O. cuniculus*, the studied suburban and urban populations show typical adaptations which previously have been reported for other urban exploiters, e. g., reduced anti-predator behavior. An important outcome of my research is that predominantly suburban habitats as areas of intermediate intensity of urbanization provide rabbits an advantageous combination of structural heterogeneity plus a comparatively low level of human disturbance and predation risk. In accordance with studies on rabbit ecology in other European countries; I argue, that future plans for rural land management actions should aim to increase refuge availability by generating networks of ecotones (LEES & BELL 2008, GUERRERO-CASADO ET AL. 2013, FERREIRA ET AL. 2014). This would also benefit species that depend on similar ecosystem structures and are on decline in Germany as the northern lapwing, *Vanellus vanellus* (BAUER & BERTHOLD 1996) or the gray partridge, *Perdix perdix* (BUNER ET AL. 2005).

My research is a first case study and some questions remained unresolved, e. g., whether urbanization first led to smaller group sizes (due to relaxed predation pressure and milder temperatures) and as a consequence of this, burrow structures changed or *vice versa*. Moreover, I was not able to disentangle the relative importance of factors that influence population dynamics, e. g., mortality rates due to disease transmission, traffic etc. In general, I emphasis the importance of future approaches that compare the ecology of one species between different urban and suburban environments over a long-term period also integrating aspects of other natural and social sciences, e. g., the management of human-wildlife conflicts. This last mentioned aspect of how urban wildlife is perceived by humans is doubtlessly a very important factor as the human disconnection from nature is the main cause for all kind of mindless habitat destruction and exploitations of natural resources.

Scientific outreach, additional results

How urbanization affects the health of wildlife is a very intriguing research topic, but in most cases can only be investigated through an invasive methodological approach. Since rabbits in and around Frankfurt were killed in any case during the hunting season, I decided to collect physiological and morphological data of 40 urban and 35 rural individuals between October 2012 and February 2013. Immediately after animals were professionally killed by hunters, they were weighted and sexed as well as blood and feces samples were taken and stored on ice. In cooperation with PD Dr Elke Schleucher and Birgit Nagel of the former working group "Animal Physiology" (Goethe University Frankfurt) blood characteristics as hematocrit, hemoglobin, plus the proportion of blood cells like leucocytes and monocytes were assessed. The carcasses were stored at $-20\,^{\circ}\mathrm{C}$ and individually defrosted before dissections. The lengths and weights of organs, as well as the presence of ecto- and endoparasites have been assessed and a calorimetric measurement of the stomach contents has been performed. Additionally, I checked for pregnancy status and the size of male testes as an indicator for fertility. Feces samples to determine base-level stress hormone values, and blood samples to measure acute stress responses were stored at $-80\,^{\circ}\mathrm{C}$. According to Augusteyn (2007) rabbits' age was determined by drying and weighing eye lenses. Finally, samples of liver, kidney, lung and heart were send to the Friedrich-Löffler-Institut Riems and were checked for hunter viruses in the laboratory of PD Dr Rainer Ulrich. The results of this approach will allow me to get a deeper understanding of how density-dependent (e. g., transmission of parasites) and density-independent factors (e. g., food quality) influence the health status of urban rabbits compared to rural populations.

In habitats where access to food and shelter-providing structures is limited, European rabbits need to overcome greater distances and thus, have larger home ranges (Gibb 1993, Moreno & Villafuerte 1995, Devillard et al. 2008). During the breeding season, for example, when high quality food becomes a crucial resource, animals' home ranges can vary from 1 ha in areas where land-use diversity is high and where food and shelter is available in close proximity (Kolb 1991) to several hectares in poorer habitats, e. g., 7.1 ha in moorland and rough pastures (Daniels et al. 2003). Many studies discovered urban populations to have smaller home ranges in comparison to their rural conspecifics (in white-tailed deer: Etter et al. 2002 or raccoons: Prange et al. 2004) but, to date no data are available for urban rabbits. For the first time, I was able to collect sufficient location fixes (in and outside of the burrows) of four females and two males at a green area within the city center of Frankfurt and of four females and four males at a large park at the suburban periphery from March to September 2012 (reproduction time). The calculated home range sizes were the smallest ever reported for this mammal

(95 % kernels ± SE, urban: 0.69 ± 0.19 ha; suburban: 0.57 ± 0.15 ha) while a general linear model (GLM) did not revealed differences between the urban and suburban study sites. These results emphasize the conclusion I drew from my previous research: urban and suburban landscapes provide food and shelter in close proximity to each other due to a high habitat heterogeneity. Home ranges of wildlife in cities tend not only to be smaller but also more stable over time because the high food supply over winter reduces the necessity for home range expansion or migration (in birds: JOKIMÄKI ET AL. 1996). Therefore, besides equipping more individuals with radio collars in order to compensate 18 % failure of radio tags, future tracking studies within the urban environment should also follow collared individuals over a longer period of time.

Habitat fragmentation within cities can lead to genetically highly structured populations because streets and buildings limit animals' migration – even over short distances and for otherwise very mobile species (WANDELER ET AL. 2003, DELANEY ET AL. 2010, GARROWAY & SHELDON 2013). Urban populations are thus often characterized by lower genetic heterogeneity in comparison to populations at rather rural landscapes (in wrentits, *Chamaea fasciata*: DELANEY ET AL. 2010 or song sparrows, *Melospiza melodia* UNFRIED ET AL. 2012) and are therefore more affected by local extinction (DELANEY ET AL. 2010). In order to find out if rabbits migrate between habitats of different urbanization levels at a regular basis, I analyzed the DNA (extracted from tissue) of 129 animals from nine differently categorized study sites by means of ten microsatellite markers. The first analyses that were run in the program STRUCTURE v2.3.3 (PRITCHARD ET AL. 2000, method presented by EVANNO ET AL. 2005) revealed no significant correlation between pairwise genetic distances and the degree of urbanity, i. e., no genetic differentiation was detected between populations within urban, suburban or rural habitats. The fact that I was able to radio-track rabbits that crossed streets above and below ground is one explanation for why I found no genetic structuring along the rural-to-urban gradient. Ongoing analyses include more fine-scaled landscape parameters, e. g., information on hunting activities, to test for conditions that shape rabbit migration and reveal the origin of the considered urban and suburban populations. These upcoming data will help to understand whether populations in cities indeed might serve as future source-populations and thus, will play an important role in the preservation of the rabbit in Germany.

In their native distribution range rabbits are regarded as "ecosystem engineers" because they positively affect soil conditions through digging activities and distribute plant seeds through their grazing and latrine-use behavior (WILLOTT ET AL. 2000, DELIBES-MATEOS ET AL. 2008, BRAVO ET AL. 2009). Dr Britta Kunz from the working group "Plant Ecology" (Goethe University Frankfurt) coordinated the collection of rabbit fecal pellets from central and peripheral latrines at five study sites of different urbanity levels in and around Frankfurt. These pellets were induced to germinate under controlled laboratory conditions and seedlings were then identified. Moreover, the adhesive properties of the different plant seeds found in latrines were tested, i. e., a known amount of seeds was applied to rabbit fur which was clasped between two wooden boards and shacked for a determined amount of time. The seeds that fell off the fur were quantified (for a more detailed description see COUVREUR ET AL. 2004). The data of this study, that for the first time aims to link plant-compositions in latrines ("fertile islands"), seed dispersal abilities and ranging behavior of rabbits within the urban and suburban habitat are currently analyzed.

References

ADAMS CE (2016). *Urban Wildlife Management*. CRC press.

ADAMS LW (2014). History of Urban Wildlife Conservation. In: *Urban Wildlife Conservation*. Springer, pp. 11–31.

ADAMS RA, LENGAS BJ & BEKOFF M (1987). Variations in avoidance responses to humans by black-tailed prairie dogs (*Cynomys ludovicianus*). *Journal of Mammalogy*, 68:686–689.

ADKINS CA & STOTT P (1998). Home ranges, movements and habitat associations of red foxes *Vulpes vulpes* in suburban Toronto, Ontario, Canada. *Journal of Zoology*, 244:335–346.

ALBERTI M (2005). The effects of urban patterns on ecosystem function. *International Regional Science Review*, 28:168–192.

ALBERTI M, BOTSFORD E & COHEN A (2001). Quantifying the urban gradient: linking urban planning and ecology. In: *Avian Ecology and Conservation in an urbanizing World*. Springer, pp. 89–115.

ALBERTI M, MARZLUFF JM, SHULENBERGER E, BRADLEY G, RYAN C & ZUMBRUNNEN C (2003). Integrating humans into ecology: opportunities and challenges for studying urban ecosystems. *BioScience*, 53:1169–1179.

ALDREDGE RA, LECLAIR SC & BOWMAN R (2012). Declining egg viability explains higher hatching failure in a suburban population of the threatened Florida scrub-jay *Aphelocoma coerulescens*. *Journal of Avian Biology*, 43:369–375.

ANGULO E & VILLAFUERTE R (2004). Modelling hunting strategies for the conservation of wild rabbit populations. *Biological Conservation*, 115:291–301.

ARMOUR CJ & THOMPSON HV (1955). Spread of myxomatosis in the first outbreak in Great Britain. *Annals of Applied Biology*, 43:511–518.

ARNOLD JM, GREISER G, KEULING O, MARTIN I & STRAUSS E (2013). Status und Entwicklung ausgewählter Wildtierarten in Deutschland. Jahresbericht 2012. Wildtier-Informationssystem der Länder Deutschlands (WILD).

Arnold W (1988). Social thermoregulation during hibernation in alpine marmots (*Marmota marmota*). *Journal of Comparative Physiology B*, 158:151–156.

Augusteyn RC (2007). On the relationship between rabbit age and lens dry weight: improved determination of the age of rabbits in the wild. *Molecular Vision*, 13:2030–4.

Baker PJ & Harris S (2007). Urban mammals: what does the future hold? An analysis of the factors affecting patterns of use of residential gardens in Great Britain. *Mammal Review*, 37:297–315.

Barrio IC, Acevedo P & Tortosa FS (2010). Assessment of methods for estimating wild rabbit population abundance in agricultural landscapes. *European Journal of Wildlife Research*, 56:335–340.

Bauer HG & Berthold P (1996). *Die Brutvögel Mitteleuropas: Bestand und Gefährdung*. Aula-Verlag.

Bell DJ (1977). *Aspects of the social behavior of wild and domesticated rabbits (Oryctolagus cuniculus)*. Ph.D. thesis, University of Wales, Cardiff.

Blair RB (1999). Birds and butterflies along an urban gradient: surrogate taxa for assessing biodiversity? *Ecological Applications*, 9:164–170.

Blair RB & Johnson EM (2008). Suburban habitats and their role for birds in the urban–rural habitat network: points of local invasion and extinction? *Landscape Ecology*, 23:1157–1169.

Bravo LG, Belliure J & Rebollo S (2009). European rabbits as ecosystem engineers: warrens increase lizard density and diversity. *Biodiversity and Ccnservation*, 18:869–885.

Brown JS, Laundré JW & Gurung M (1999). The ecology of fear: optimal foraging, game theory, and trophic interactions. *Journal of Mammalogy*, 80:385–399.

Buner F, Jenny M, Zbinden N & Naef-Daenzer B (2005). Ecologically enhanced areas–a key habitat structure for re-introduced grey partridges *Perdix perdix*. *Biological Conservation*, 124:373–381.

Burger J & Gochfeld M (2009). Exotic monk parakeets (*Myiopsitta monachus*) in New Jersey: nest site selection, rebuilding following removal, and their urban wildlife appeal. *Urban Ecosystems*, 12:185–196.

Calvete C, Estrada R, Angulo E & Cabezas-Ruiz S (2004). Habitat factors related to wild rabbit conservation in an agricultural landscape. *Landscape Ecology*, 19:531–542.

Carrete M & Tella JL (2009). Individual consistency in flight initiation distances in burrowing owls: a new hypothesis on disturbance-induced habitat selection. *Biology Letters*, 6:167–70.

Chapman T, Rymer T & Pillay N (2012). Behavioural correlates of urbanisation in the Cape ground squirrel *Xerus inauris*. *Naturwissenschaften*, 99:893–902.

Contesse P, Hegglin D, Gloor S, Bontadina F & Deplazes P (2004). The diet of urban foxes (*Vulpes vulpes*) and the availability of anthropogenic food in the city of Zurich, Switzerland. *Mammalian Biology - Zeitschrift für Säugetierkunde*, 69:81–95.

Couvreur M, Vandenberghe B, Verheyen K & Hermy M (2004). An experimental assessment of seed adhesivity on animal furs. *Seed Science Research*, 14:147–159.

Cowan DP (1984). The use of ferrets (*Mustela furo*) in the study and management of the European wild rabbit (*Oryctolagus cuniculus*). *Journal of Zoology*, 204:570–574.

Cowan DP (1987). Group living in the european rabbit (*Oryctolagus cuniculus*): mutual benefit or resource localization? *Journal of Animal Ecology*, 56:779–795.

Cresswell WJ & Harris S (1988). Foraging behavior and home range utilization in a suburban badger (*Meles meles*). *Mammal Review*, 18:37–49.

Czech B, Krausman PR & Devers PK (2000). Economic Associations among causes of species endangerment in the United States. *BioScience*, 50:593–601.

Daniels MJ, Lees JD, Hutchings MR & Greig A (2003). The ranging behaviour and habitat use of rabbits on farmland and their potential role in the epidemiology of paratuberculosis. *The Veterinary Journal*, 165:248–257.

Davison J, Huck M, Delahay R & Roper TJ (2008). Urban badger setts: characteristics, patterns of use and management implications. *Journal of Zoology*, 275:190–200.

Davison J, Huck M, Delahay RJ & Roper TJ (2009). Restricted ranging behaviour in a high-density population of urban badgers. *Journal of Zoology*, 277:45–53.

Dearborn DC & Kark S (2010). Motivations for conserving urban biodiversity. *Conservation Biology*, 24:432–440.

Delaney KS, Riley SP & Fisher RN (2010). A rapid, strong, and convergent genetic response to urban habitat fragmentation in four divergent and widespread vertebrates. *PLoS One*, 5:e12767.

Delibes-Mateos M, Delibes M, Ferreras P & Villafuerte R (2008). Key role of European Rabbits in the conservation of the western mediterranean basin hotspot. *Conservation Biology*, 22:1106–1117.

Delibes-Mateos M, Farfán MÁ, Olivero J & Vargas JM (2010). Land-use changes as a critical factor for long-term wild rabbit conservation in the Iberian Peninsula. *Environmental Conservation*, 37:169–176.

Devillard S, Aubineau J, Berger F, Léonard Y, Roobrouck A & Marchandeau S (2008). Home range of the European rabbit (*Oryctolagus cuniculus*) in three contrasting French populations. *Mammalian Biology - Zeitschrift für Säugetierkunde*, 73:128–137.

Dip R, Hegglin D, Deplazes P, Dafflon O, Koch H & Naegeli H (2003). Age-and sex-dependent distribution of persistent organochlorine pollutants in urban foxes. *Environmental Health Perspectives*, 111:1608–1612.

Ditchkoff SS, Saalfeld ST & Gibson CJ (2006). Animal behavior in urban ecosystems: modifications due to human-induced stress. *Urban Ecosystems*, 9:5–12.

Domínguez-Cebrían I & de Miguel FJ (2013). Selected factors influencing the spatial relationship between latrines and burrows in rabbits *Oryctolagus cuniculus* (L.) in a suburban area of Madrid (Spain). *Polish Journal of Ecology*, 61:819–823.

Dröscher I & Kappeler PM (2014). Maintenance of familiarity and social bonding via communal latrine use in a solitary primate (*Lepilemur leucopus*). *Behavioral Ecology and Sociobiology*, 68:2043–2058.

Duduś L, Zalewski A, Koziol O, Jakubiec Z & Król N (2014). Habitat selection by two predators in an urban area: The stone marten and red fox in Wrocław (SW Poland). *Mammalian Biology - Zeitschrift für Säugetierkunde*, 79:71–76.

Edmondson JL, Davies ZG, McCormack SA, Gaston KJ & Leake JR (2011). Are soils in urban ecosystems compacted? A citywide analysis. *Biology Letters*, 7:771–774.

Eisermann K (1992). Long-term heartrate responses to social stress in wild European rabbits: Predominant effect of rank position. *Physiology & Behavior*, 52:33–36.

Endlicher W, Langner M, Hesse M, Mieg HA, Kowarik I, Hostert P, Kulke E, Nützmann G, Schulz M, van der Meer E et al. (2007). Urban ecology–definitions and concepts. In: *Shrinking cities: effects on urban ecology and challenges on urban development*. pp. 1–13.

Estes WA & Mannan RW (2003). Feeding behavior of Cooper's Hawks at urban and rural nests in southeastern Arizona. *The Condor*, 105:107–116.

Etter DR, Hollis KM, Van Deelen TR, Ludwig DR, Chelsvig JE, Anchor CL & Warner RE (2002). Survival and movements of white-tailed deer in suburban Chicago, Illinois. *Journal of Wildlife Management*, 66:500–510.

Evanno G, Regnaut S & Goudet J (2005). Detecting the number of clusters of individuals using the software STRUCTURE: a simulation study. *Molecular Ecology*, 14:2611–2620.

Evans J, Boudreau K & Hyman J (2010). Behavioural syndromes in urban and rural populations of song sparrows. *Ethology*, 116:588–595.

Ferreira C, Touza J, Rouco C, Díaz-Ruiz F, Fernandez-de Simon J, Ríos-Saldaña CA, Ferreras P, Villafuerte R & Delibes-Mateos M (2014). Habitat management as a generalized tool to boost European rabbit *Oryctolagus cuniculus* populations in the Iberian Peninsula: a cost-effectiveness analysis. *Mammal Review*, 44:30–43.

Fischer JD, Cleeton SH, Lyons TP & Miller JR (2012). Urbanization and the predation paradox: the role of trophic dynamics in structuring vertebrate communities. *BioScience*, 62:809–818.

Fleischer ALJ, Bowman R & Woolfenden GE (2003). Variation in foraging behavior, diet, and time of breeding of Florida scrub-jays in suburban and wildlife habitats. *Condor*, 105:515–527.

Fleming MR (1980). Thermoregulation and torpor in the sugar glider, *Petaurus Breviceps* (Marsupialia: Petauridae). *Australian Journal of Zoology*, 28:521–534.

Forman RTT (2008). *Urban regions: ecology and planning beyond the city*. Cambridge University Press.

Forman RTT & Alexander LE (1998). Roads and their major ecological effects. *Annual Review of Ecology and Systematics*, 29:207–231.

French SS, Fokidis HB & Moore MC (2008). Variation in stress and innate immunity in the tree lizard (*Urosaurus ornatus*) across an urban–rural gradient. *Journal of Comparative Physiology B*, 178:997–1005.

Frid A & Dill LM (2002). Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology*, 6:11.

Garroway CJ & Sheldon BC (2013). Urban behavioural adaptation. *Molecular Ecology*, 22:3430–3432.

Gea-Izquierdo G, Muñoz-Igualada J & San Miguel-Ayanz A (2005). Rabbit warren distribution in relation to pasture communities in Mediterranean habitats: consequences for management of rabbit populations. *Wildlife Research*, 32:723–731.

Gehrt S (2004). Ecology and management of striped skuns, raccoons, and coyotes in urban landscapes. In: Fascione N, Delach A & Smith M (eds.) *People and predators: from conflict to coexistence*. Washington US, pp. 81–104.

Gehrt SD (2007). *Urban coyote ecology and management: the Cook County, Illinois, coyote project.* Ohio State University Extension.

George SL & Crooks KR (2006). Recreation and large mammal activity in an urban nature reserve. *Biological Conservation*, 133:107–117.

Getz LL, Best LB & Prather M (1977). Lead in urban and rural song birds. *Environmental Pollution (1970)*, 12:235–238.

Gibb JA (1993). Sociality, time and space in a sparse population of rabbits (*Oryctolagus cuniculus*). *Journal of Zoology*, 229:581–607.

Gloor S, Bontadina F, Hegglin D, Deplazes P & Breitenmoser U (2001). The rise of urban fox populations in Switzerland. *Mammalian Biology - Zeitschrift für Säugetierkunde*, 66:155–164.

Goddard MA, Dougill AJ & Benton TG (2010). Scaling up from gardens: biodiversity conservation in urban environments. *Trends in Ecology & Evolution*, 25:90–98.

Grimm NB, Faeth SH, Golubiewski NE, Redman CL, Wu J, Bai X & Briggs JM (2008). Global change and the ecology of cities. *Science*, 319:756–760.

Guerrero-Casado J, Carpio AJ, Ruiz-Aizpurua L & Tortosa FS (2013). Restocking a keystone species in a biodiversity hotspot: Recovering the European rabbit on a landscape scale. *Journal for Nature Conservation*, 21:444–448.

Hadidian J & Smith S (2001). Urban Wildlife. In: Salem D (ed.) *The State of the Animals: 2001.* Humane Society of the US.

Harper SJ & Batzli GO (1996). Effects of predators on structure of the burrows of voles. *Journal of Mammalogy*, 77:1114–1121.

Harris S (1982). Activity patterns and habitat utilization of badgers (*Meles meles*) in suburban Bristol: a radio tracking study. *Symposium of the Zoological Society of London*, 49:301–323.

Harris S (1984). Ecology of Urban badgers *Meles meles*: distribution in Britain and habitat selection, persecution, food and damage in the city of Bristol. *Biological Conservation*, 28:349–375.

Herr J, Schley L, Engel E & Roper TJ (2010). Den preferences and denning behaviour in urban stone martens (*Martes foina*). *Mammalian Biology - Zeitschrift für Saugetierkunde*, 75:138–145.

Hesterman ER & Mykytowycz R (1982). Misidentification by wild rabbits, *Oryctolagus cuniculus*, of group members carrying the odor of foreign inguinal gland secretion. *Journal of Chemical Ecology*, 8:419–427.

von Holst D, Hutzelmeyer H, Kaetzke P, Khaschei M, Rödel HG & Schrutka H (2002). Social rank, fecundity and lifetime reproductive success in wild European rabbits (*Oryctolagus cuniculus*). *Behavioral Ecology and Sociobiology*, 51:245–254.

Hutchings MR, Service KM & Harris S (2002). Is population density correlated with faecal and urine scent marking in European badgers (*Meles meles*) in the UK? *Mammalian Biology – Zeitschrift für Säugetierkunde*, 67:286–293.

Iossa G, Soulsbury C, Baker P & Harris S (2010). A taxonomic analysis of urban carnivore ecology. In: Gehrt S, Riley S & Cypher B (eds.) *Urban Carnivores*. The John Hopkins University Press: Baltimore, MD, pp. 173–180.

Irwin MT, Samonds KE, Raharison JL & Wright PC (2004). Lemur latrines: observations of latrine behavior in wild primates and possible ecological significance. *Journal of Mammalogy*, 85:420–427.

Jokimäki J, Suhonen J, Inki K & Jokinen S (1996). Biogeographical comparison of winter bird assemblages in urban environments in Finland. *Journal of Biogeography*, 23:379–386.

Jokimäki J & Suhonen J (1998). Distribution and habitat selection of wintering birds in urban environments. *Landscape and Urban Planning*, 39:253–263.

Jordan NR, Cherry MI & Manser MB (2007). Latrine distribution and patterns of use by wild meerkats: implications for territory and mate defence. *Animal Behaviour*, 73:613–622.

Kark S, Iwaniuk A, Schalimtzek A & Banker E (2007). Living in the city: can anyone become an "urban exploiter"? *Journal of Biogeography*, 34:638–651.

Klausnitzer B (1989). *Verstädterung von Tieren*. Neue Brehm-Bücherei, Wittenberg-Lutherstadt.

Kolb HH (1985). The burrow structure of the European rabbit (*Oryctolagus cuniculus L.*). *Journal of Zoology*, 206:253–262.

Kolb HH (1991). Use of burrows and movements of wild rabbits (*Oryctolagus cuniculus*) in an area of hill grazing and forestry. *Journal of Applied Ecology*, 28:892–905.

Kontsiotis V, Bakaloudis D, Xofis P, Konstantaras N, Petrakis N & Tsiompanoudis A (2013). Modeling the distribution of wild rabbits (*Oryctolagus cuniculus*) on a Mediterranean island. *Ecological Research*, 28:317–325.

Kowarik I (2011). Novel urban ecosystems, biodiversity, and conservation. *Environmental Pollution*, 159:1974–1983.

Krebs CJ (1999). *Ecological methodology*. Addison Wesley, Longman Inc., Menlo Park, California, 2nd edition.

Kruuk H (1995). *Wild otters predation and population*. University Press Oxford.

Kruuk H (1978). Spatial organization and territorial behaviour of the European badger *Meles meles*. *Journal of Zoology*, 184:1–19.

Kübler S, Kupko S & Zeller U (2005). The kestrel (*Falco tinnunculus* L.) in Berlin: investigation of breeding biology and feeding ecology. *Journal of Ornithology*, 146:271–278.

Lees AC & Bell DJ (2008). A conservation paradox for the 21st century: the European wild rabbit *Oryctolagus cuniculus*, an invasive alien and an endangered native species. *Mammal Review*, 38:304–320.

Lefebvre L (1986). Cultural diffusion of a novel food-finding behaviour in urban pigeons: An experimental field test. *Ethology*, 71:295–304.

Lehrer E, Schooley R & Whittington J (2011). Survival and antipredator behavior of woodchucks (*Marmota monax*) along an urban–agricultural gradient. *Canadian Journal of Zoology*, 90:12–21.

Lepczyk CA, Mertig AG & Liu J (2004). Landowners and cat predation across rural-to-urban landscapes. *Biological Conservation*, 115:191–201.

Lombardi L, Fernández N, Moreno S & Villafuerte R (2003). Habitat-related differences in rabbit (*Oryctolagus cuniculus*) abundance, distribution, and activity. *Journal of Mammalogy*, 84:26–36.

Lombardi L, Fernández N & Moreno S (2007). Habitat use and spatial behaviour in the European rabbit in three Mediterranean environments. *Basic and Applied Ecology*, 8:453–463.

Loucks OL (1994). Sustainability in urban ecosystems: beyond an object of study. *The Ecological City University of Massachusetts Press, Amherst, Massachusetts, USA*, 65.

Luniak M (2004). Synurbization - adaptation of animal wildlife to urban development. In: Shaw WW, Harris LK & Vandruff L (eds.) *4th International Urban Wildlife Symposium.* pp. 50–55.

MacGregor-Fors I (2011). Misconceptions or misunderstandings? On the standardization of basic terms and definitions in urban ecology. *Landscape and Urban Planning*, 100:347–349.

Magle SB & Angeloni LM (2011). Effects of urbanization on the behaviour of a keystone species. *Behaviour*, 148:31–54.

Magle SB, Hunt VM, Vernon M & Crooks KR (2012). Urban wildlife research: past, present, and future. *Biological Conservation*, 155:23–32.

Magle SB, Theobald DM & Crooks KR (2009). A comparison of metrics predicting landscape connectivity for a highly interactive species along an urban gradient in Colorado, USA. *Landscape Ecology*, 24:267–280.

Marks CA & Bloomfield TE (2006). Home-range size and selection of natal den and diurnal shelter sites by urban red foxes (*Vulpes vulpes*) in Melbourne. *Wildlife Research*, 33:339–347.

Marzluff JM, Bowman R & Donnelly R (2001). A historical perspective on urban bird research: trends, terms, and approaches. In: Marzluff JM, Bowman R & Donnelly RE (eds.) *Avian Conservation and Ecology in an Urbanizing World*. Springer US, pp. 1–17.

McCleery RA (2009). Changes in fox squirrel anti-predator behaviors across the urban-rural gradient. *Landscape Ecology*, 24:483–493.

McCleery RA, Lopez RR, Silvy NJ & Gallant DL (2008). Fox squirrel survival in urban and rural environments. *The Journal of Wildlife Management*, 72:133–137.

McCleery RA, Moorman CE & Peterson MN (2014). *Urban Wildlife Conservation*. Springer US.

McClennen N, Wigglesworth RR, Anderson SH & Wachob DG (2001). The effect of suburban and agricultural development on the activity patterns of coyotes (*Canis latrans*). *The American Midland Naturalist*, 146:27–36.

McDonald RI, Kareiva P & Forman RTT (2008). The implications of current and future urbanization for global protected areas and biodiversity conservation. *Biological Conservation*, 141:1695–1703.

McDonnell MJ & Hahs AK (2008). The use of gradient analysis studies in advancing our understanding of the ecology of urbanizing landscapes: current status and future directions. *Landscape Ecology*, 23:1143–1155.

McDonnell MJ & Pickett STA (1990). Ecosystem structure and function along urban-rural gradients: an unexploited opportunity for ecology. *Ecology*, 71:1232–1237.

McDonnell MJ, Pickett STA & Pouyat RV (1993). The application of the ecological gradient paradigm to the study of urban effects. In: *Humans as components of ecosystems: subtle human effects and the ecology of populated areas*. Springer New York, pp. 175–189.

McHale MR, Pickett STA, Barbosa O, Bunn DN, Cadenasso ML, Childers DL, Gartin M, Hess GR, Iwaniec DM, McPhearson T, Peterson MN, Poole AK, Rivers L, Shutters ST & Zhou W (2015). The new global urban realm: complex, connected, diffuse, and diverse social-ecological systems. *Sustainability*, 7:5211–5240.

McKinney ML (2002). Urbanization, biodiversity, and conservation. *BioScience*, 52:883–890.

McKinney ML (2006). Urbanization as a major cause of biotic homogenization. *Biological Conservation*, 127:247–260.

McKinney ML (2008). Effects of urbanization on species richness: a review of plants and animals. *Urban Ecosystems*, 11:161–176.

McKinney ML & Lockwood JL (1999). Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in Ecology & Evolution*, 14:450–453.

Meffert PJ & Dziock F (2012). What determines occurrence of threatened bird species on urban wastelands? *Biological Conservation*, 153:87–96.

Miller JR & Hobbs RJ (2002). Conservation where people live and work. *Conservation Biology*, 16:330–337.

Møller AP (2008). Flight distance of urban birds, predation, and selection for urban life. *Behavioral Ecology and Sociobiology*, 63:63–75.

Møller AP (2009). Successful city dwellers: a comparative study of the ecological characteristics of urban birds in the Western Palearctic. *Oecologia*, 159:849–858.

Monclús R & de Miguel FJ (2003). Distribución espacial de las letrinas de conejo (*Oryctolagus cuniculus*) en el Monte de Valdelatas (Madrid). *Galemys*, 15:157–165.

Moreno S, Beltrán JF, Cotilla I, Kuffner B, Laffite R, Jordán G, Ayala J, Quintero C, Jiménez A, Castro F et al. (2008). Long-term decline of the European wild rabbit (*Oryctolagus cuniculus*) in south-western Spain. *Wildlife Research*, 34:652–658.

Moreno S & Villafuerte R (1995). Traditional management of scrubland for the conservation of rabbits *Oryctolagus cuniculus* and their predators in Doñana National Park, Spain. *Biological Conservation*, 73:81–85.

Myers K & Poole WE (1959). A study of the biology of the wild rabbit, *Oryctolagus cuniculus* (L.), in confined populations. I. The effects of density on home range and the formation of breeding groups. *CSIRO Wildlife Research*, 4:14–26.

Mykytowycz R (1962). Territorial function of chin gland secretion in the rabbit, *Oryctolagus cuniculus* (L.). *Nature*, 193:799.

Mykytowycz R & Gambale S (1969). The distribution of dung-hills and the behaviour of freeliving wild rabbits, *Oryctolagus cuniculus* (L.), on them. *Forma et Functio*, 1:333–349.

Mykytowycz R & Hesterman ER (1970). The behaviour of captive wild rabbits, *Oryctolagus cuniculus* (L.) in response to strange dung-hills. *Forma et Functio*, 2:1–12.

Mykytowycz R, Hestermann ER, Gambale S & Dudziński ML (1976). A comparison of the effectiveness of the odors of rabbits, *Oryctolagus cuniculus*, in enhancing territorial confidence. *Journal of Chemical Ecology*, 2:13–24.

Nemeth E & Brumm H (2009). Blackbirds sing higher-pitched songs in cities: adaptation to habitat acoustics or side-effect of urbanization? *Animal Behaviour*, 78:637–641.

Niemelä J (1999). Ecology and urban planning. *Biodiversity & Conservation*, 8:119–131.

Oke TR (1982). The energetic basis of the urban heat island. *Quarterly Journal of the Royal Meteorological Society*, 108:1–24.

Palomares F (2001). Comparison of 3 methods to estimate rabbit abundance in a mediterranean environment. *Wildlife Society Bulletin*, 29:578–585.

Partecke J, Schwabl I & Gwinner E (2006). Stress and the city: urbanization and its effects on the stress physiology in European blackbirds. *Ecology*, 87:1945–1952.

Partecke J, Van't Hof T & Gwinner E (2004). Differences in the timing of reproduction between urban and forest European blackbirds (*Turdus merula*): result of phenotypic flexibility or genetic differences? *Proceedings of the Royal Society*, 271:1995–2001.

Pickett ST, Cadenasso ML, Grove JM, Boone CG, Groffman PM, Irwin E, Kaushal SS, Marshall V, McGrath BP, Nilon CH et al. (2011). Urban ecological systems: scientific foundations and a decade of progress. *Journal of Environmental Management*, 92:331–362.

Pickett ST, Cadenasso ML, Grove JM, Nilon CH, Pouyat RV, Zipperer WC & Costanza R (2008). Urban ecological systems: linking terrestrial ecological, physical, and socioeconomic components of metropolitan areas. In: *Urban Ecology*. Springer US, pp. 99–122.

Planillo A & Malo JE (2013). Motorway verges: paradise for prey species? A case study with the European rabbit. *Mammalian Biology - Zeitschrift für Säugetierkunde*, 78:187–192.

Prange S & Gehrt SD (2004). Changes in mesopredator-community structure in response to urbanization. *Canadian Journal of Zoology*, 82:1804–1817.

Prange S, Gehrt SD & Wiggers EP (2003). Demographic factors contributing to high raccoon densities in urban landscapes. *The Journal of Wildlife Management*, 67:324–333.

Prange S, Gehrt SD & Wiggers EP (2004). Influences of anthropogenic resources on raccoon (*Procyon lotor*) movements and spatial distribution. *Journal of Mammalogy*, 85:483–490.

Pritchard JK, Stephens M & Donnelly P (2000). Inference of population structure using multilocus genotype data. *Genetics*, 155:945–959.

Prugh LR, Stoner CJ, Epps CW, Bean WT, Ripple WJ, Laliberte AS & Brashares JS (2009). The rise of the mesopredator. *Bioscience*, 59:779–791.

Qureshi S, Haase D & Coles R (2014). The theorized urban gradient (TUG) method–a conceptual framework for socio-ecological sampling in complex urban agglomerations. *Ecological Indicators*, 36:100–110.

Ralls K & Smith DA (2004). Latrine use by San Joaquin kit foxes (*Vulpes macrotis mutica*) and coyotes (*Canis latrans*). *Western North American Naturalist*, 64:544–547.

Ramalho CE & Hobbs RJ (2012). Time for a change: dynamic urban ecology. *Trends in Ecology & Evolution*, 27:179–188.

Rödel HG & Dekker JJ (2012). Influence of weather factors on population dynamics of two lagomorph species based on hunting bag records. *European Journal of Wildlife Research*, 58:923–932.

Rebele F (1994). Urban ecology and special features of urban ecosystems. *Global Ecology and Biogeography Letters*, 4:173–187.

Riley SPD, Sauvajot RM, Fuller TK, York EC, Kamradt DA, Bromley C & Wayne RK (2003). Effects of urbanization and habitat fragmentation on bobcats and coyotes in southern California. *Conservation Biology*, 17:566–576.

Riley SPD, Serieys LE & Moriarty JG (2014). Infectious disease and contaminants in urban wildlife: unseen and often overlooked threats. In: *Urban Wildlife Conservation*. Springer US, pp. 175–215.

Risch M, Dwenger A & Wirth H (1996). Der Sperber (*Accipiter nisus*) als Brutvogel in Hamburg: Bestandsentwicklung und Bruterfolg 1982–1996. *Hamburger Avifaunistische Beiträge*, 28:43–57.

Rödel HG, Bora A, Kaetzke P, Khaschei M, Hutzelmeyer H & Von Holst D (2004). Over-winter survival in subadult European rabbits: weather effects, density dependence, and the impact of individual characteristics. *Oecologia*, 140:566–576.

Rodewald AD & Bakermans MH (2006). What is the appropriate paradigm for riparian forest conservation? *Biological Conservation*, 128:193–200.

Rodewald AD & Gehrt SD (2014). Wildlife population dynamics in urban landscapes. In: *Urban Wildlife Conservation*. Springer US, pp. 117–147.

Roper TJ, Conradt L, Butler J, Christian SE, Ostler J & Schmid TK (1993). Territorial marking with faeces in badgers (*Meles meles*): a comparison of boundary and hinterland latrine use. *Behaviour*, 127:289–307.

Rutz C (2006). Home range size, habitat use, activity patterns and hunting behaviour of urban-breeding Northern Goshawks *Accipiter gentilis*. *Ardea*, 94:185.

Ryan AM & Partan SR (2014). Urban wildlife behavior. In: *Urban Wildlife Conservation*. Springer US, pp. 149–173.

Schieber P (1983). *Untersuchungen über Wildkaninchen im Stadtgebiet Münchens*. Ph.D. thesis.

Schley L, Schaul M & Roper T (2004). Distribution and population density of badgers *Meles meles* in Luxembourg. *Mammal Review*, 34:233–240.

Seto KC, Güneralp B & Hutyra LR (2012). Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. *Proceedings of the National Academy of Sciences*, 109:16083–16088.

Shepherd JM, Stallins JA, Jin ML & Mote TL (2010). Urbanization: impacts on clouds, precipitation, and lightning. *Urban Ecosystem Ecology*:1–27.

Shochat E (2004). Credit or debit? Resource input changes population dynamics of city-slicker birds. *Oikos*, 106:622–626.

Shulenberger E, Endlicher W, Bradley G, Ryan C, ZumBrunnen C, Simon U, Marzluff J et al. (2008). *Urban ecology: an international perspective on the interaction between humans and nature*. Springer US.

Sih A, Ferrari MCO & Harris DJ (2011). Evolution and behavioural responses to human-induced rapid environmental change. *Evolutionary Applications*, 4:367–387.

Sih A, Stamps J, Yang LH, McElreath R & Ramenofsky M (2010). Behavior as a key component of integrative biology in a human-altered world. *Integrative and Comparative Biology*, 50:934–944.

Fernandez-de Simon J, Diaz-Ruiz F, Villafuerte R, Delibes-Mateos M & Ferreras P (2011). Assessing predictors of pellet persistence in European rabbits *Oryctolagus cuniculus*: towards reliable population estimates from pellet counts. *Wildlife Biology*, 17:317–325.

Slabbekoorn H & Peet M (2003). Ecology: birds sing at higher pitch in urban noise. *Nature*, 424:267.

Smith AT & Boyer AF (2008). *Oryctolagus cuniculus*. The IUCN red list of threatened species 2008:. www.iucnredlist.org. Version 2010.4.

Sneddon IA (1991). Latrine use by the European Rabbit (*Oryctolagus cuniculus*). *Journal of Mammalogy*, 72:769–775.

Stewart PD, Macdonald DW, Newman C & Cheeseman CL (2001). Boundary feaces and matched advertisement in the European badger (*Meles meles*): a potential role in range exclusion. *Journal of Zoology*, 255:191–198.

Strasser EH & Heath JA (2013). Reproductive failure of a human-tolerant species, the American kestrel, is associated with stress and human disturbance. *Journal of Applied Ecology*, 50:912–919.

Sukopp H (1998). *Urban ecology—scientific and practical aspects*. Springer Berlin Heidelberg.

Tarlow EM & Blumstein DT (2007). Evaluating methods to quantify anthropogenic stressors on wild animals. *Applied Animal Behaviour Science*, 102:429–451.

Tuomainen U & Candolin U (2011). Behavioural responses to human-induced environmental change. *Biological Reviews*, 86:640–657.

Uchida K, Suzuki K, Shimamoto T, Yanagawa H & Koizumi I (2015). Seasonal variation of flight initiation distance in Eurasian red squirrels in urban versus rural habitat. *Journal of Zoology*, 298:225–231.

Unfried TM, Hauser L & Marzluff JM (2012). Effects of urbanization on Song Sparrow (*Melospiza melodia*) population connectivity. *Conservation Genetics*, 14:41–53.

UNPD (2014). United Nations Population Division, 2014. World Urbanization Prospects: The 2014 Revision. New York, accessed 24.11.2016, http://esa.un.org/unpd/wup/CDRom/Urban-Rural-Population.htm.

Villafuerte R, Calvete C, Blanco JC & Lucientes J (1995). Incidence of viral hemorrhagic disease in wild rabbit populations in Spain. *Mammalia*, 59:651–660.

Villafuerte R & Moreno S (1997). Predation risk, cover type, and group size in European rabbits in Doñana (SW Spain). *Acta Theriologica*, 42:225–230.

Virgós E, Cabezas-Díaz S, Malo A, Lozano J & López-Huertas D (2003). Factors shaping European rabbit abundance in continuous and fragmented populations of central Spain. *Acta Theriologica*, 48:113–122.

Wandeler P, Funk SM, Largiader C, Gloor S & Breitenmoser U (2003). The city-fox phenomenon: genetic consequences of a recent colonization of urban habitat. *Molecular Ecology*, 12:647–656.

Willott SJ, Miller AJ, Incoll LD & Compton SG (2000). The contribution of rabbits (*Oryctolagus cuniculus* L.) to soil fertility in semi-arid Spain. *Biology and Fertility of Soils*, 31:379–384.

Wronski T, Apio A & Plath M (2006). The communicatory significance of localised defecation sites in bushbuck (*Tragelaphus scriptus*). *Behavioral Ecology and Sociobiology*, 60:368–378.

Wronski T, Apio A, Plath M & Ziege M (2013). Sex difference in the communicatory significance of localized defecation sites in Arabian gazelles (*Gazella arabica*). *Journal of Ethology*, 31:129–140.

Wronski T & Plath M (2010). Characterization of the spatial distribution of latrines in reintroduced mountain gazelles: do latrines demarcate female group home ranges? *Journal of Zoology*, 280:92–101.

Wu JJ (2008). Making the case for landscape ecology an effective approach to urban sustainability. *Landscape Journal*, 27:41–50.

Wu JJ (2014). Urban ecology and sustainability: the state-of-the-science and future directions. *Landscape and Urban Planning*, 125:209–221.

Zhang C, Wu J, Grimm NB, McHale M & Buyantuyev A (2013). A hierarchical patch mosaic ecosystem model for urban landscapes: model development and evaluation. *Ecological Modelling*, 250:81–100.

Ziege M, Babitsch D, Brix M, Kriesten S, Seidemann A, Wenninger S & Plath M (2013). Anpassungsfähigkeit des Europäischen Wildkaninchens entlang eines rural-urbanen Gradienten. *Beiträge zur Jagd- und Wildforschung*, 38:189–199.

Ziege M, Babitsch D, Brix M, Kriesten S, Straskraba S, Wenninger S, Wronski T & Plath M (2016a). Extended diurnal activity patterns of European rabbits along a rural-to-urban gradient. *Mammalian Biology - Zeitschrift für Säugetierkunde*, 81:534–541.

Ziege M, Bierbach D, Bischoff S, Brandt AL, Brix M, Greshake B, Merker S, Wenninger S, Wronski T & Plath M (2016b). Importance of latrine communication in European rabbits shifts along a rural-to-urban gradient. *BMC Ecology*, 16:29.

Ziege M, Brix M, Schulze M, Seidemann A, Straskraba S, Wenninger S, Streit B, Wronski T & Plath M (2015). From multifamily residences to studio apartments: shifts in burrow structures of European rabbits along a rural-to-urban gradient. *Journal of Zoology*, 295:286–293.

Zipperer WC, Wu J & Pouyat STA R Vand Pickett (2000). The application of ecological principles to urban and urbanizing landscapes. *Ecological Application*, 10:685–688.

Chapter 2

Quantifying the degree of urbanization and its effects on population densities of the European rabbit.

This chapter consists of the following publication:

Ziege M, Babitsch D, Brix M, Kriesten S, Seidemann A, Straskraba S, Wenninger S & Plath M (2013). Anpassungsfähigkeit des Europäischen Wildkaninchens entlang eines rural-urbanen Gradienten. *Beiträge zur Jagd- und Wildforschung*, 38:189-199.

Ziege, Brix and Plath designed the theoretical framework. Ziege, Babitsch, Brix, Kriesten, Seidemann, Straskraba and Wenninger collected and analyzed data. Ziege and Plath wrote and corrected the manuscript. More details on contributions of me and my co-authors are given below in the form "Anlage 1: Ausführungsbestimmungen für Dissertationen im Promotionsfach Biologie, die bereits veröffentlichte Teile oder eingereichte Manuskripte enthalten".

Anlage 1

Erklärung zu den Autorenanteilen

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Beiträge zur
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Madlen Ziege, Denise Babitsch, Mareike Brix, Stefanie Kriesten, Axel Seidemann,
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Anpassungsfähigkeit des Europäischen Wildkaninchens (*Oryctolagus cuniculus*) entlang eines rural-urbanen Gradienten

Schlagworte/keywords: Wildkaninchen, *Oryctolagus cuniculus*, Urbanisierung, Fluchtverhalten, Verhaltensanpassung, Habituation, Urbanisation, flight distance, behavioural adaptation, habituation

Einleitung

Wildschweine in Berlin, Waschbären in Kassel oder Siebenschläfer in Osnabrück – in den letzten Jahren häufen sich die Meldungen über Wildtiere in deutschen Städten wie auch weltweit. Die intensive menschliche Nutzung und Überformung natürlicher Lebensräume führt zu deren Degradierung und zwingt Wildtiere, die in diesen Lebensräumen vorkommen, in andere Gebiete abzuwandern (Marzluff et al. 2001). Insbesondere die immer weiter fortschreitende Urbanisierung zieht eine Zerstörung und Fragmentierung natürlicher Lebensräume nach sich und trägt somit entscheidend zum Verlust von Biodiversität bei (Antrop 2003, Hansen et al. 2005). Andererseits stellen moderne Städte mit ihren spezifischen biotischen und abiotischen Bedingungen durchaus alternative Lebensräume für Tier- und Pflanzenarten dar (Francis & Chadwick 2012) und werden hinsichtlich der Erhaltung der biologischen Vielfalt zukünftig eine besondere Rolle einnehmen (Ditchkoff et al. 2006).

Neben den zahlreichen freien ökologischen Nischen, die aus den vielfältigen Nutzungsarten/-intensitäten hervorgehen (Møller 2008), zeichnet sich das urbane Ökosystem vor allem durch einen konstant hohen Zugang zu Nahrungsressourcen (Ditchkoff et al. 2006), ein milderes Mikroklima (Wessolek 2008) sowie einem geringeren Prädations- und Jagddruck aus (Baker & Harris 2007, Fischer et al. 2012). Diese besonderen Bedingungen scheinen natürliche Selektionsprozesse teilweise „abzupuffern“, und es liegt der Schluss nahe, dass Wildtiere in der Stadt weniger Stress ausgesetzt sein könnten als ihre ruralen Artgenossen (Luniak 2004, Ditchkoff et al. 2006). Andererseits werden Wildtiere in urbanen Gebieten mit anthropogen verursachten Störfaktoren wie Verkehr, Lärm, künstlichen Lichtverhältnissen, Luftverschmutzung, sowie der ständigen Präsenz von Menschen konfrontiert (Partecke et al. 2006, Kowarik 2011). Zeit und Energie, die durch (unnötige) Fluchtreaktionen aufgewendet werden müssen, stehen einem Organismus nicht mehr für andere Funktionsbereiche wie die Nahrungsaufnahme, die Suche nach einem geeigneten Reproduktionspartner oder die Jungenaufzucht zur Verfügung. Somit sind Individuen, die im städtischen Raum weniger sensitiv auf die Störung durch Menschen reagieren, im Vorteil gegenüber Artgenossen, die permanente

Fluchtreaktionen zeigen. Dass es hier zu Habituationsprozessen kommt, zeigt die Studie von Møller (2008), in der kürzere Fluchtinitiationsdistanzen für urbane Populationen einheimischer Vogelarten im Vergleich zu ruralen Populationen gemessen wurden. Ähnliche Beobachtungen wurden auch für Fuchshörnchen (*Scirius niger*) gemacht (McCleery 2009).

Der städtische Lebensraum stellt somit eine vom Menschen geprägte selektive Umgebung dar, in der solche Individuen bessere Überlebenschancen haben, die flexibel auf diese neuartigen Bedingungen mit plastischen (also nicht erblich bedingten) Verhaltensunterschieden reagieren. Angesichts der Zunahme der in Städten lebenden menschlichen Bevölkerung wird sich die Urbanisierung zukünftig weiter ausdehnen und es werden solche Tier- und Pflanzenarten aus ihren Lebensräumen verdrängt, die nicht mit den neuen, vom Menschen geschaffenen Bedingungen zurecht kommen. Eine entscheidende Frage ist daher, warum einige Arten in der Lage sind sich erfolgreich im städtischen Lebensraum zu etablieren, während andere es nicht können und welche Mechanismen dieser Variation zu Grunde liegen. Insbesondere hinsichtlich möglicher Konflikte zwischen Wildtieren und der städtischen Bevölkerung müssen langfristig Pläne für ein nachhaltiges Management erstellt werden. Dies kann nur basierend auf ausreichenden Kenntnissen über Populationsdichten und -dynamiken, spezifischen Verhaltensweisen oder physiologischen Charakteristika von Wildtieren in der Stadt erfolgen (Ditchkoff et al. 2006). Obwohl sich wissenschaftliche Untersuchungen in den letzten Jahren zunehmend mit dieser Thematik auseinandersetzen, ist bisher nur für wenige Arten hinreichend dokumentiert worden, welchen Einfluss das „Großstadtleben“ tatsächlich auf Wildtiere hat.

Das Europäische Wildkaninchen ist in Mitteleuropa ein typischer Kulturfolger, der häufig in urbanen Gebieten wie Parkanlagen oder Friedhöfen vorkommt. Innerhalb des natürlichen Verbreitungsgebiets (Nordwest-Afrika und Spanien) verzeichnet der Bestand von *O. cuniculus* starke Einbrüche und wird deshalb von der IUCN (*International Union for Conservation of Nature*) auf der Vorwarnliste als „gering gefährdet“ („*near-threatened*“, Smith & Boyer 2008) geführt. Mit der Ausbreitung der Viruserkrankung Myxomatose ab dem Jahre 1952 bzw. der Chinaseuche (*Rabbit Haemorrhagic Disease*, RHD) in den 1980er Jahren hat auch der Bestand des Europäischen Wildkaninchens in Deutschland stark abgenommen. Im Rahmen der letzten flächendeckenden Bestandsschätzung durch das Wildtierinformationssystem der deutschen Bundesländer meldeten 34 % der beteiligten Jagdbezirke nur noch geringe Besätze (< 10 Individuen/100 ha). Das Europäische Wildkaninchen ist, laut Aussage von Herrn R. Pirzkall, Landesbetreuer des Jagdverbandes Mecklenburg-Vorpommern, in ländlichen Bereichen Mecklenburg-Vorpommerns gegenwärtig sogar noch weitaus seltener geworden als das Rebhuhn (*Perdix perdix*); Restbestände finden sich ausnahmslos nur noch in Städten (bezogen auf ein Telefonat im September 2011). Auch in den anderen deutschen Bundesländern hat die Zahl der jährlich erlegten Wildkaninchen stetig abgenommen (siehe auch Rödel & Dekker 2012). Umso paradoxer erscheint diese Situation, wenn man die Verbreitung von Wildkaninchen in den Städten betrachtet, in denen manchmal gar von einer „Kaninchenplage“ gesprochen wird. Zuständige Behörden stehen vor dem Problem des Managements von Wildkaninchen in den Grünanlagen, die durch das Anlegen von Bauten und den Verbiss an Gehölzen finanzielle Schäden verursachen. Dieses Management sieht in vielen deutschen Städten die jährliche Bejagung der Tiere von Oktober bis März mit Frettchen und Greifvögeln vor. Derzeit gibt es keine wissenschaftlichen Erkenntnisse darüber, wie sich die verbliebenen Bestände in den außerstädtischen Lebensräumen entwickeln werden und ob die Tiere in den Städten zukünftig als „*source*“-Populationen eine Bedeutung für den Erhalt dieser Wildtierart in Deutschland erhalten könnten.

Ziel dieser Studie war es, Populations- und Bautendichten sowie Fluchtinitiationsdistanzen von Wildkaninchenpopulationen entlang eines rural-urbanen Gradienten in Frankfurt am Main bzw. dessen Umland zu erfassen. Mit zunehmendem Urbanitätsgrad gewinnen auch Bedingungen an Bedeutung, die zu einem schnellen Anstieg von Wildtierpopulationen bzw. zur Abpufferung von negativen Populationsdynamiken führen können (z. B. wärmeres Mikroklima, erhöhter Nahrungszugang oder fehlende Prädation). Unsere Annahme war daher, dass die Kaninchen- bzw. Bautendichte positiv mit dem Urbanitätsgrad korreliert.

Im Zuge der Anpassung an die ständige Präsenz anthropogener Störungen erwarteten wir zudem einen negativen Zusammenhang zwischen Fluchtinitiationsdistanzen und dem Grad der Urbanisierung.

Methoden

Bestimmung des Urbanitätsgrades

Unabhängig von ihrer spezifischen Struktur folgen urbane Lebensräume gewöhnlich einem konsistenten Muster: Im Stadtzentrum erreichen anthropogene Einflüsse bzw. die Präsenz des Menschen ein Maximum. Präsenz und Einfluss nehmen jedoch kontinuierlich in Richtung ruraler, weniger entwickelter Gebiete ab (Adams 1994). Dieser landschaftliche Übergang wird als urban-ruraler Gradient bezeichnet (McDonnell & Pickett 1990).

Basierend auf diesem Gradienten wurden folgende Studiengebiete innerhalb der Habitate „urban“, „suburban“ und „rural“ ausgewählt: Die ehemalige innere Wallanlage im Zentrum der Stadt Frankfurt am Main stellte das urbane Habitat dar (N 50°7,049‘ O 8°40,623; ca. 26 ha). In acht der insgesamt neun, durch stark befahrene Straßen voneinander getrennten, unterschiedliche große Grünanlagen befinden sich Wildkaninchenpopulationen. Jede dieser Populationen wurde als eine unabhängige Stichprobe für den Urbanitätsgrad „urban“ angesehen. Das „suburbane“ Habitat wurde durch 5 Parkbereiche repräsentiert, die sich in der angrenzenden Umgebung des Stadtzentrums befinden: Ostpark (N 50°7,251 O 8°43,364; ca. 30,2 ha), Rebstockpark (N 50°6,674 O 8°36,773; ca. 21,1 ha), Miquelanlage (N 50°7,967 O 8°39,590; ca. 5,5 ha), Grüneburgpark (N 50°7,621 O 8°39,630; ca. 27,0 ha) und Elli-Lucht-Park (N 50°5,386 O 8°38,853; ca. 2,9 ha). Die Auswahl der ruralen Studiengebiete erfolgte durch Hinweise auf Wildkaninchenbestände durch die örtliche Jägerschaft. Diese Gebiete befinden sich in der ländlichen, vorwiegend agrarwirtschaftlich genutzten Peripherie der Frankfurter Vororte Kriftel (N 50°4,546 O 8°27,835), Bad Vilbel (N 50°9,886 O 8°41,850) und Maintal (N 50°8,653 O 8°49,094) sowie dem zwischen Darmstadt und Frankfurt gelegenen Götzenhain (N 50°0,305‘ O 8°43,421). Innerhalb dieser Gebiete wurden je zwei 700 x 700 m Quadranten zufällig ausgewählt.

Chadwick & Francis (2012) weisen darauf hin, dass Untersuchungen zu möglichen Anpassungs- oder Habituationsprozessen von Wildtieren entlang eines rural-urbanen Gradienten lokale Variabilität im Urbanisierungsgrad einbeziehen sollten. Laut der Studie von MacGregor-Fors (2011) ist die Bestimmung des Anteils der vom Menschen geschaffenen, versiegelten Oberflächen im relevanten Studiengebiet ein guter Indikator für den Urbanitätsgrad. Eine standardisierte Herangehensweise zur quantitativen Erfassung des Urbanitätsgrads im Zusammenhang mit der Untersuchung von Wildtierpopulationen ist uns derzeit nicht bekannt (siehe dazu auch McDonnel & Hahs 2008). Die vorliegende Studie bediente sich der Berechnung eines „Urbanitätsindex“, der sich aus folgenden Variablen zusammensetzt:

1. Anwohnerdichte im Umkreis von 500 m, ausgehend vom Rand des Studiengebietes (in Kooperation mit dem Einwohnermeldeamt der Stadt Frankfurt am Main, Stand: 31.10.2010);
2. prozentualer Anteil der vom Menschen geschaffenen, versiegelten Flächen im Studiengebiet (Gebäude, Straßen, etc.) mittels des von der Stadt Frankfurt zur Verfügung gestellten Kartenmaterials und dem Programm ArcGIS 10;
3. Anzahl anthropogen geschaffener Objekte pro ha (Bänke, Straßenlaternen etc.) im Studiengebiet;
4. Anzahl der durch Menschen (Fußgänger, Fahrradfahrer) und angeleinte sowie freilaufende Hunde erfolgten Störungen pro min pro ha durch Transektzählungen zu den Hauptaktivitätszeiten der Wildkaninchen. Es erfolgten 10 Zählungen in der Morgen- und 10 in der Abenddämmerung bzw. kurz nach Sonnenuntergang an jeweils 5 aufeinander folgenden Tagen. Nach dem Zufallsprinzip wurden Koordinaten im Studiengebiet ausgewählt, von denen ausgehend entlang virtu-

eller Transekte (25 m lang, 10 m breit, nach Norden weisend) für 3 Minuten alle Personen, Fahrradfahrer bzw. Hunde erfasst wurden, die das Transekt kreuzten. Es erfolgten zwei Zählungen im Abstand von ca. 30 min. Die Anzahl der Transekte berücksichtigte die Größe der Studiengebiete. Alle Zählungen in den verschiedenen Gebieten erfolgten in einem vergleichbaren Zeitraum im Sommer 2011.

Diese 4 Variablen wurden einer Hauptkomponentenanalyse mittels SPSS 13 unterzogen. Es ergab sich eine Hauptkomponente mit einem Eigenwert > 1, die 66,65 % der Gesamtvarianz erklärte und als Urbanitätsindex verwendet wurde.

Populations- und Bautendichte

Palomares (2001) fasste in seiner Studie die Vor- und Nachteile unterschiedlicher Herangehensweisen zur Quantifizierung von Kaninchendichten zusammen. Neben der Erfassung der Bautendichte und direkten Zählungen kann die Bestandsdichte auch indirekt über die Anzahl von Kotpellets in definierten Quadranten bestimmt werden. In dieser Studie wurden ebenfalls verschiedene methodische Herangehensweisen kombiniert, um repräsentative Daten zur Kaninchendichte zum Ende der Reproduktionszeit im September/Anfang Oktober 2011 zu erheben. Die direkte Bestandserfassung erfolgte durch Zählungen mittels Scheinwerfern eine Stunde nach Sonnenuntergang entlang von Transekten, die in 30 m Abständen durch das gesamte Studiengebiet verliefen (siehe Palomares 2001, Calvete et al. 2004). Je nach Größe der Studiengebiete wurden die Transekte von mehreren Personen gleichzeitig abgelaufen, mindestens jedoch von zwei Personen. Kaninchensichtungen entlang der Transekte wurden auf einer Karte notiert. Pro Studiengebiet erfolgten je zwei Zählungen an zwei aufeinanderfolgenden Tagen. Auf Grund ungünstiger Witterungsbedingungen lagen in einigen Fällen mehrere Tage zwischen der ersten und zweiten Erfassung. Im Rahmen einer Verhaltensstudie erfolgten im vergleichbaren Zeitraum jeweils zwei gezielte Beobachtungen an den Bauten bzw. im Umkreis von 50 m zur Dämmerungszeit bzw. nach Sonnenuntergang. Es wurde darauf geachtet, dass vergleichbare Wetterbedingungen während der Beobachtungen am Bau herrschten.

Im Rahmen einer umfassenden Studie zur Bautenstruktur, deren Analyse noch andauert, konnte auch die Bautendichte in den relevanten Studiengebieten bestimmt werden. Dies erfolgte im urbanen, suburbanen und teilweise im ruralen Studiengebiet während der Jagdsaison 2011/12 in Zusammenarbeit mit dem Frankfurter Stadtjäger Axel Seidemann. Zur Bejagung der Wildkaninchen werden Frettchen und Reusen eingesetzt. Die Frettchen treiben dabei die Wildkaninchen aus dem Bau und in die zuvor vor den Bauöffnungen positionierten Reusen. Diese Jagdart erlaubte es, zuverlässig einzelne Bauten voneinander abzugrenzen und somit die Bautendichte in den einzelnen Studiengebieten zu bestimmen.

Diese Herangehensweise war jedoch nicht bei allen Bauten möglich (z. B. aus jagdrechtlichen Gründen). Ein einzeln abzugrenzender Bau wurde in diesem Fall durch die Position der Ein- und Ausgänge definiert. Alle beieinanderliegenden Bautenöffnungen, deren Gänge in das Zentrum des vermeintlichen Baues wiesen, gehörten auch mit hoher Wahrscheinlichkeit zu diesem Bau.

Fluchtverhalten

Die Messung der Fluchtinitiationsdistanzen in den verschiedenen Studiengebieten erfolgte nach dem Protokoll von Møller (2008) im Sommer 2011. Der Beobachter bewegte sich aus einer Ausgangsentfernung von 50 m mit Schrittgeschwindigkeit auf das zufällig ausgewählte Wildkaninchen zu (Jungtiere wurden nicht berücksichtigt). Die Distanz, bei der das Tier die Flucht ergriff (gerichtetes Wegbewegen vom ursprünglichen Standort) wurde mit Hilfe eines Laserentfernungsmessgerätes (Bosch GLM 150) ermittelt und notiert. Zudem wurde vermerkt, ob das beobachtete Individuum allein oder in der Gruppe war. Es wurde sorgfältig darauf geachtet, dass Individuen nicht mehrfach getestet wurden, was die vergleichsweise geringe Stichprobengröße im ruralen Studiengebiet erklärt.

Statistische Auswertung

(a) Populations- und Bautendichte

Um zu testen, ob es einen statistisch abzusichernden Zusammenhang zwischen dem Urbanisierungsgrad (Hauptkomponente 1, s.o.) und der Populations- bzw. Bautendichte gibt, wurde eine Spearman Rangkorrelation durchgeführt.

(b) Fluchtinitiationsdistanzen

Eine Spearman Rangkorrelation sollte auch prüfen, ob es einen signifikanten Zusammenhang zwischen dem Urbanisierungsgrad und der Fluchtinitiationsdistanz gibt. Zudem wurde eine univariate ANOVA durchgeführt, um weiter zu testen, ob es mögliche Unterschiede im Fluchtverhalten zwischen ruralen, urbanen und suburbanen Populationen gibt.
Abhängige Variable war die Fluchtinitiationsdistanz, der unabhängige Faktor der Urbanitätsgrad sowie das Studiengebiet (genestet in den Faktor Urbanitätsgrad) sowie der bivariate Faktor ‚sozialer Kontext' (0 = allein, 1 = in einer Gruppe).

Ergebnisse

Populations- und Bautendichte

Die Spearman Rangkorrelation ergab einen signifikanten, positiven Zusammenhang zwischen dem Urbanitätsgrad (Hauptkomponente 1) und der Populationsdichte (r = 0,557; $P \leq 0{,}001$; N = 68) bzw. der Anzahl der Bauten pro ha (r = 0,614; P = 0,015; N = 16) (Abb. 1, 2).

Fluchtinitiationsdistanz

Die Ergebnisse der univariaten ANOVA zeigten, dass sich die Fluchtinitiationsdistanzen sowohl zwischen den drei Urbanitätsniveaus urban, suburban und rural, als auch zwischen den einzelnen Studiengebieten signifikant unterscheiden (Tabelle 1). Hingegen hatten die Variablen ‚sozialer Kontext' bzw. der Interaktionsterm ‚Urbanitätsgrad × sozialer Kontext' keinen Einfluss auf die Fluchtdistanzen und wurden daher aus dem finalen Modell ausgeschlossen. Die folgende Spearman Rangkorrelation zeigte einen signifikanten, negativen Zusammenhang zwischen dem Urbanitätsgrad und den Fluchtinitiationsdistanzen auf (r = -0,517; $P \leq 0.001$; N = 246; Abbildung 3).

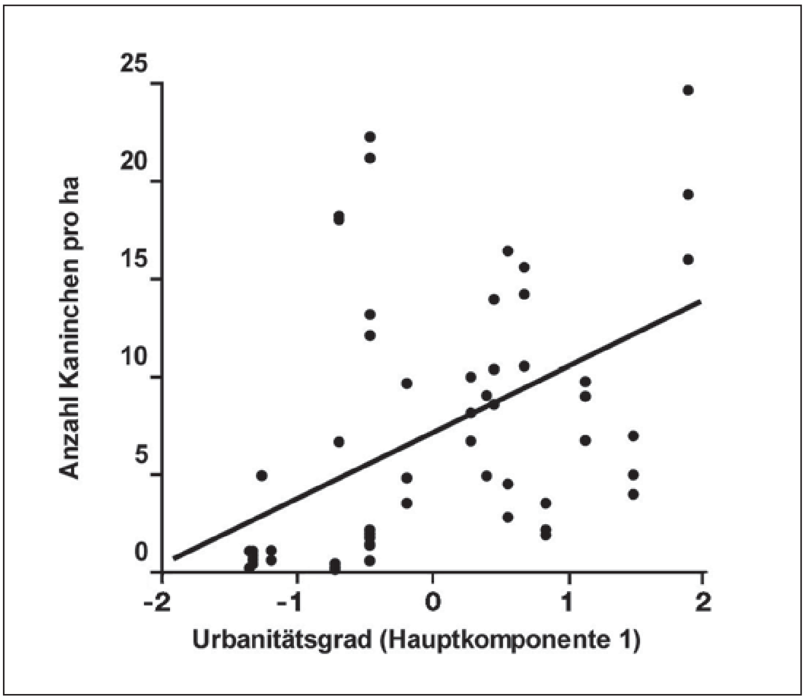

Abb. 1 Positive Korrelation zwischen der Kaninchendichte (Anzahl der Tiere pro ha) im September und Oktober 2011 und dem Urbanitätsgrad. Die durchgeführte Spearman Rangkorrelation zeigt eine signifikante Abhängigkeit: r = 0,558; P ≤ 0,001; N = 68.

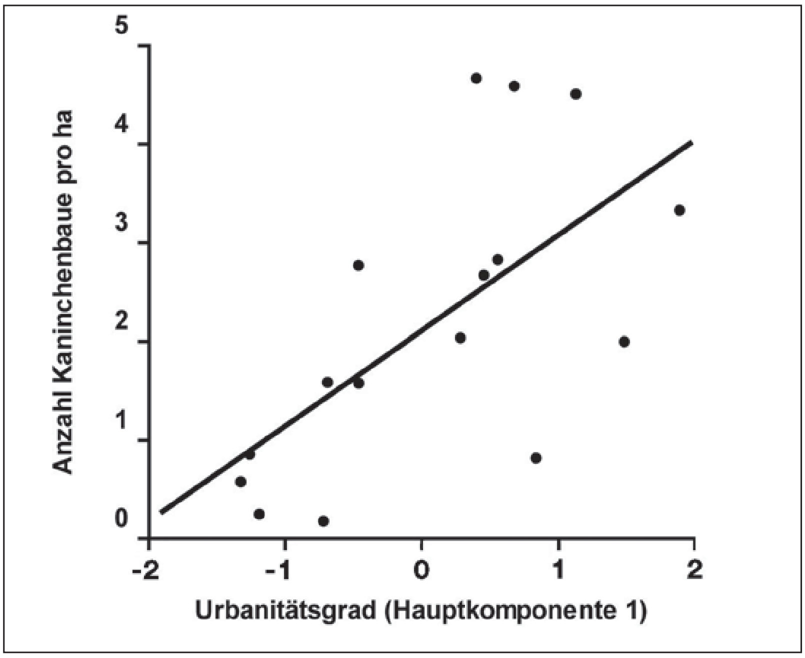

Abb. 2 *Positive Korrelation zwischen der Bautendichte (Anzahl der Baue pro ha im Studiengebiet) und dem Urbanitätsgrad. Die Spearman Rangkorrelation zeigt eine signifikante Abhängigkeit: r = 0,629; P = 0,009; N = 17.*

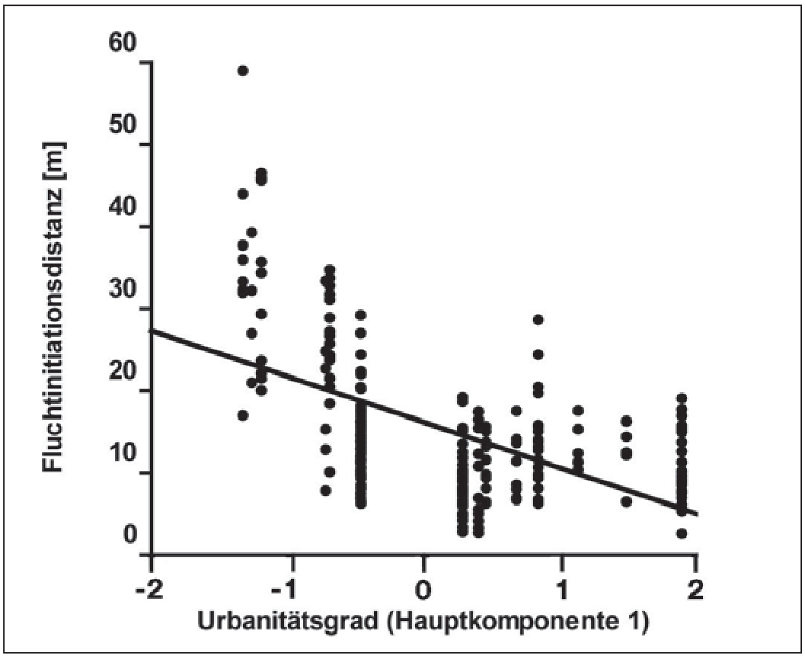

Abb. 3 *Negative Korrelation zwischen der individuellen Fluchtinitiationsdistanz [m] und dem Urbanitätsgrad. Spearman Rangkorrelation: r = -0,519; P ≤ 0,001; N = 239.*

Tabelle 1 Ergebnisse der univariaten ANOVA mit der abhängigen Variable „Fluchtinitiationsdistanz" und den unabhängigen Variablen Urbanitätsgrad bzw. Studiengebiet (genestet in den Faktor Urbanitätsgrad), sowie ‚sozialer Kontext'.

Effekt	*F*	Fehler *df*	Quadratischer Mittelwert	*P*	Partielle Varianz
Achsenschnittstelle	1576,725	1	50912,990	≤ 0,001	0,877
Urbanitätsgrad	143,546	2	4635,140	≤ 0,001	0,564
Studiengebiet (Urbanitätsgrad)	5,581	13	180,221	≤ 0,001	0,246

Diskussion

Das Vorkommen von Wildtieren in städtischen und randstädtischen Lebensräumen ist keine Ausnahmeerscheinung mehr. Häufig stellt der urbane Raum mit seinen vielfältigen ökologischen Nischen sogar letzte Rückzugsmöglichkeiten für gefährdete Tier- und Pflanzenarten dar. Dies scheint auch auf das Europäische Wildkaninchen (*Oryctolagus cuniculus*) zuzutreffen, dessen Bestände in Deutschland sich derzeit in vielen Bundesländern fast ausschließlich auf den urbanen Raum beschränken. Am Beispiel der Stadt Frankfurt am Main und ihrer Umgebung konnten wir zeigen, dass Kaninchen- bzw. Bautendichten tatsächlich entlang des rural-urbanen Gradienten zunehmen. Dieser Trend lässt sich durch mehrere Faktoren erklären.

Kalte Winter in Kombination mit einem niederschlagsreichen Frühjahr reduzieren die Überlebenswahrscheinlichkeit von Wildkaninchen (Rödel et al. 2004, Rödel & Dekker 2012). Zwar fällt im urbanen Raum mehr Niederschlag als im Umland, aber die direkte Oberflächenabführung des Regenwassers erlaubt nur noch wenig Verdunstung. Die zunehmende Bebauung entlang des rural-urbanen Gradienten resultiert in einem Temperaturanstieg, der ein trockeneres Mikroklima in Städten weiter begünstigt (Wessolek 2008). In Kombination mit dem Überfluss an Nahrung wirken sich die wärmeren Temperaturen positiv auf das Reproduktionspotential, die Dauer der Vegetations- bzw. Wachstumsperiode (Klausnitzer 1989) sowie auf die Überlebenswahrscheinlichkeit einiger Säugetierarten aus (z. B. den Waschbären, *Procyon lotor*, Prange et al. 2003 oder das Fuchshörnchen, *Sciurus niger*, McCleery et al. 2008).

Bereits 1983 wies Schieber darauf hin, dass für Wildkaninchen im Münchener Stadtgebiet die Reproduktionsperiode früher zu beginnen scheint, als es für Wildkaninchen im ländlichen Habitat bekannt war. Ähnliche Beobachtungen wurden auch für die untersuchten Populationen in Frankfurt am Main gemacht. Neben der Verlängerung der Reproduktionsperiode (bei Vögeln: Fleischer et al. 2003) kann auch die Anzahl der Nachkommen pro Wurf zunehmen (bei Ratten: Robbins 1993). Fehlende Ausbreitungsmöglichkeiten der Jungtiere in geeignete Habitate lassen spezifische Populationsdichten lokal weiter ansteigen (z. B. beim Dachs, *Meles meles*: Davison et al. 2009).

Allerdings können anthropogene Faktoren in Städten den Reproduktionserfolg bzw. die Überlebenswahrscheinlichkeit von Organismen auch negativ beeinflussen. So spielt die Akkumulation künstlicher Futterquellen eine wichtige Rolle bei der Übertragung von Krankheiten (Smith & Engeman 2002) bzw. kann der Verkehr in der Stadt zu einer erhöhten Sterblichkeitsrate führen (Forman & Alexander 1998). Auch wenn der Prädation durch natürliche Raubfeinde im urbanen Raum weniger Bedeutung zuzumessen ist (Fischer 2012), können Hunde oder Katzen in der Stadt als neue, nichtnatürliche Prädatoren auftreten (Lepczyk et al. 2004). Zudem sind Organismen im urbanen Raum dem Ausstoß von Schadstoffen aus Verkehr und Industrie ausgesetzt (z. B. Füchse: Dip et al. 2003). In welchem Maße diese Faktoren Wildkaninchenpopulationen beeinflussen, ist derzeit noch nicht bekannt.

Neben den bereits genannten biotischen und abiotischen Faktoren, die einen schnellen Anstieg der Wildtierdichten entlang des rural-urbanen Gradienten begünstigen, sei an diese Stelle auf die heterogene Habitatstruktur städtischer Siedlungsbereiche hingewiesen. Das für Städte typische „Habitatmosaik“ bietet Lebensraum für Tier- und Pflanzenarten mit den unterschiedlichsten ökologischen Ansprüchen (Møller 2008). Auch für die Verbreitung von Wildkaninchenpopulationen ist bekannt, dass sich eine diverse Landnutzung positiv auf die Kaninchendichte auswirkt (Rogers and Myers 1979, Villafuerte and Moreno 1997, Kontsiotis et al. 2013). Dabei bietet der von Wildkaninchen bevorzugte Lebensraum sowohl Zugang zu ausreichend Nahrung als auch zu schützender Vegetation in nächster Nähe zu den Nahrungsgründen (Gibb 1993).

Im Gegensatz zum urbanen Habitat zeichnen sich rurale Lebensräume in Mitteleuropa im Zuge der modernen agrarwirtschaftlichen Nutzung überwiegend durch Offenlandschaften bzw. eine landschaftliche Homogenisierung aus. Diese Entwicklung hat nachweislich einen negativen Einfluss auf die Populationsdichten vieler Wildtierarten (Kiebitz, *Vanellus vanellus*:

Bauer & Berthold 1996; Rebhuhn, *Perdix perdix*: Buner et al. 2005).

Gegenwärtige Methoden zur Quantifizierung des Einflusses anthropogener Faktoren auf Wildtiere umfassen neben der Bestimmung der Populationsdichten auch die Messung von Fluchtinitiationsdistanzen (Tarlow & Blumstein 2007). Bisherige Studien bezogen sich dabei auf kategorische Vergleiche der Fluchtinitiationsdistanzen zwischen urbanen, ruralen und suburbanen Individuen einer Art (z. B. Fuchshörnchen: McCleery 2009). Die von uns durchgeführte ANOVA bestätigte die Annahme, dass es signifikante Unterschiede in der Fluchtreaktion zwischen ruralen, urbanen und suburbanen Wildkaninchenpopulationen gibt. Die Analyse zeigte jedoch auch, dass sich die Fluchtdistanzen zwischen den einzelnen Studiengebieten innerhalb derselben Urbanitätskategorie unterscheiden. Wie bereits erwähnt, stellen städtische Räume ein komplexes Netzwerk aus Arealen mit unterschiedlich intensiver Bebauung bzw. Störungsintensitäten dar. Eine Kategorisierung in urban, suburban und rural, bezogen auf die Distanz zum Stadtzentrum (rural-urbaner Gradient, siehe Adams 1994), kann diese Variation nur grob erfassen und eignet sich somit nur bedingt zur Untersuchung von Anpassungsprozessen an die Urbanisierung (Werner, 2011).

Der von uns berechnete Urbanitätsindex berücksichtigt lokale Unterschiede in der Bebauung oder der anthropogenen Störintensität zwischen den Studiengebieten und ermöglicht eine Korrelation mit den jeweiligen individuellen Fluchtdistanzen bzw. Populations- und Bautendichten pro Untersuchungsgebiet. Verweisend auf die zusammenfassende Studie von Werner (2011) könnten zur Bestimmung des Urbanitätsgrades in Zukunft noch weitere Indikatoren berücksichtig werden: das lokale Klima (Temperatur, Niederschlag), Quantität und Qualität der vom Menschen bereitgestellten Nahrungsressourcen, Intensität der Luft-, Wasser- und Bodenverschmutzung sowie der Grad an Bodenversiegelung, der Lärmpegel oder die Intensität künstlicher Beleuchtung. Die Implementierung einer standardisierten Herangehensweise zur Berechnung eines allgemein anerkannten Urbanitätsindex wäre insbesondere bei vergleichenden Untersuchungen zur Artenvielfalt in unterschiedlichen Städten von großer Bedeutung.

Die vorliegende Studie ist als erster, kleinerer Teilaspekt einer multi-biologischen Herangehensweise an die Anpassungsfähigkeit des Europäischen Wildkaninchens entlang des rural-urbanen Gradienten zu verstehen. Derzeit dauern umfassende Untersuchungen bzw. statistische Analysen zur Populationsgenetik (Mikrosatellitenanalysen), Populationsdynamik (Dichtebestimmung über einen längeren Zeitraum, Jagdstrecken, Bautennutzung), zur Habitatnutzung (Radiotelemetrie, Bautenstrukturen) und zum Gesundheitszustand (Parasitenbefall, Blutparameter) der hier beschriebenen Kaninchenpopulationen an. Die so aus der Labor- und Feldarbeit gewonnenen Erkenntnisse sollen sowohl zur Schaffung von Grundlagenwissen beitragen als auch künftige Entscheidungen hinsichtlich eines nachhaltigen Wildtiermanagements erleichtern. Die bereits vorliegenden Ergebnisse lassen darauf schließen, dass städtische Lebensräume langfristig eine entscheidende Rolle hinsichtlich des Schutzes dieser einst so häufigen Wildtierart in Deutschland einnehmen werden.

Zusammenfassung

Der Bestand des Europäischen Wildkaninchens (*Oryctolagus cuniculus*) ist in den letzten Jahren im ländlichen Raum Deutschlands dramatisch zurückgegangen. Diese Entwicklung scheint paradox, wenn man Populationsdichten in den Städten betrachtet, in denen manchmal gar von einer „Kaninchenplage“ gesprochen wird. Aus der Diskrepanz der Bestandsentwicklung des Europäischen Wildkaninchens in Stadt und Land erwächst die Frage, inwieweit die Art tatsächlich als gefährdet angesehen werden muss. Ziel dieser Studie war es, Kaninchen- und Bautendichten entlang eines rural-urbanen Gradienten in Frankfurt am Main bzw. Umgebung zu ermitteln. Das Messen von Fluchtinitiationsdistanzen urbaner, suburbaner und ruraler Wildkaninchenpopulationen sollte zudem Aufschluss über die Anpassungsfähigkeit dieses Wildtieres gegenüber menschlichen Störungen geben. Die Populations- sowie Bautendichten nahmen mit steigendem Grad an Urbanität signifikant zu,

während Fluchtinitiationsdistanzen signifikant kürzer wurden. Wir argumentieren, dass die beobachtete Populationsdynamik insbesondere mit den spezifischen Habitatansprüchen des Europäischen Wildkaninchens in Zusammenhang gebracht werden kann. Der optimale Lebensraum dieser Wildtierart bietet sowohl Zugang zu ausreichend Nahrung als auch die Möglichkeit, in nächster Nähe Bauten anzulegen bzw. schützende Vegetation aufsuchen zu können. Diese Bedingungen finden sich in ländlichen, oft agrarwirtschaftlich genutzten Flächen mit ausgeräumten und offenen Landschaften zunehmend seltener. Urbane und suburbane Lebensräume zeichnen sich jedoch durch eine heterogene Habitatnutzung aus, die den Ansprüchen des Wildkaninchens weitaus besser entsprechen. Zudem könnten sich das wärmere Mikroklima, der konstant hohe Zugang zu Nahrungsressourcen sowie ein geringer Prädations- und Jagddruck in Städten positiv auf Wildtierdichten auswirken. Abnehmende Fluchtinitiationsdistanzen mit zunehmendem Urbanitätsgrad sind ein eindeutiger Hinweis darauf, dass Wildkaninchen im städtischen Habitat eine Habituation an die vom Menschen geschaffenen Bedingungen zeigen. Weitere Untersuchungen zur Populationsgenetik bzw. -dynamik, Habitatnutzung und zum Gesundheitszustand ruraler, urbaner und suburbaner Populationen dauern derzeit noch an. Die aus dieser multi-biologischen Herangehensweise gewonnenen Erkenntnisse sollen abschließend klären, ob urbane Wildkaninchenbestände zukünftig als „*source*"–Populationen eine Bedeutung für den Erhalt dieser Wildtierart in Deutschland einnehmen werden.

Summary

Habituation to anthropogenic nuisance of European rabbits along a rural-to-urban gradient.

Once common in Germany and representing a popular game species, population densities of the European rabbit in rural areas are currently declining at an alarming pace. At the same time, the species reaches surprisingly high population densities in urban and suburban areas. Here, rabbits often cause wildlife-human conflicts, leading to population management actions in form of hunting. Detailed knowledge about potential differences in population dynamics between urban and rural rabbit populations is necessary to establish and manage rabbit populations in the long-term. Therefore, we asked whether the degree of urbanity is indeed a predictor of rabbit and burrow densities in Frankfurt am Main and its hinterland. Additionally, we assessed flight initiation distances of rabbits along the rural-to-urban gradient to uncover potential habituation to human disturbance. We found a clear positive correlation between rabbit or burrow density and the degree of urbanity. Flight initiation distances became significantly shorter with increasing urbanity. We argue that altered habitat conditions are the major reason for why rabbits became more abundant along the rural to urban gradient. Nowadays, rural areas in Germany are typically characterized by homogenous land-use patterns, leading to consolidated, open landscapes. Aside from the more heterogeneous habitat structure arising from the diverse mosaic of buildings, parks and gardens, the urban ecosystem is characterized by constant and high food supply (human waste and deliberate feeding), a milder microclimate and lower predation or hunting pressure. These conditions are known to positively affect population densities and to buffer negative population dynamics of wildlife in cities. Our data suggest that urban habitats will play an important role in the future conservation of the European rabbit in Germany. Ongoing studies on the population genetics, population dynamics, home range use and health status of the examined rural, urban and suburban rabbit populations aim to provide additional insights into the adaptability of this mammal to urbanization.

Literatur

Adams, L.W. (1994): Urban wildlife habitats: a landscape perspective. – University Minnesota Press, Minneapolis, MN.

Antrop, M. (2003): Landscape change and the urbanization process in Europe. – Landscape and Urban Planning **67**: 9–26.

Baker, P.J.; Harris, S. (2007): Urban mammals: what does the future hold? An analysis of the factors affecting patterns of use of residential gardens in Great Britain. – Mammal Review **37**: 297–315.

Bauer, H.G.; Berthold, P. (1996): Die Brutvögel Mitteleuropas. Bestand und Gefährdung. – Wiesbaden – AULA-Verlag.

Buner, F.; Jenny, M.; Zbinden, N.; Naef-Danzer, B. (2005): Ecologically enhanced areas – a key habitat structure for re-introduced grey partridges *Perdix perdix*. – Biological Conservation **124**: 373–381.

Calvete, C.; Estrada, R.; Angulo, E.; Cabezas-Ruiz, S. (2004): Habitat factors related to wild rabbit conservation in an agricultural landscape. – Landscape Ecology **19**: 531–542.

Cresswell, W.; Harris, S. (1988): Foraging behavior and home range utilization in a suburban badger (*Meles meles*). – Mammal Review **18**: 37–49.

Davison, J.; Huck, M.; Delahay, R.J.; Roper, T.J. (2009): Restricted ranging behaviour in a high-density population of urban badgers. – Journal of Zoology **277**: 45–53.

Dip, R.; Hegglin, D.; Deplazes, P.; Dafflon, O.; Koch, H.; Naegeli, H. (2003): Age- and Sex-Dependent Distribution of Persistent Organochlorine Pollutants in Urban Foxes. – Environmental Health Perspectives **111**: 1608–1612.

Ditchkoff, S.; Saalfeld, S.; Gibson, C. (2006): Animal behavior in urban ecosystems: Modifications due to human-induced stress. – Urban Ecosystems **9**: 5–12.

Fischer, J.D.; Cleeton, S.H.; Lyons, T.P.; Miller, J.R. (2012): Urbanization and the Predation Paradox: The Role of Trophic Dynamics in Structuring Vertebrate Communities. – BioScience **62**: 809–818.

Fleischer, A.J.; Bowman, R.; Woolfenden, G. (2003): Variation in foraging behavior, diet, and time of breeding of Florida scrub-jays in suburban and wildlife habitats. – Condor **105**: 515–527.

Forman, R.; Alexander, L. (1998): Roads and their major ecological effects. – Annual Review of Ecology and Systematics **29**: 207–231.

Francis, R.A.; Chadwick, M.A. (2012): What makes a species synurbic? – Applied Geography **32**: 514–521.

Gibb, G. (1993): Sociality, time and space in a sparse population of rabbits (*Oryctolagus cuniculus)*. – Journal of Zoological Society London **229**: 581–607.

Hansen, A.; Knight, R.; Marzluff, J.; Powell, S.; Brown, K.; Gude, P.; Jones, K. (2005): Effects of Exurban Development on Biodiversity: Patterns, Mechanisms and Research Needs. – Ecological Applications **15**: 1893–1905.

Klausnitzer, B. (1989): Verstädterung von Tieren. – Neue Brehm-Bücherei Wittenberg-Lutherstadt.

Kontsiotis, V.J.; Bakaloudis, D.E.; Xofis, P.; Konstantaras, N.; Petrakis, N.; Tsiompanoudis, A. (2013): Modeling the distribution of wild rabbits (*Oryctolagus cuniculus*) on a Mediterranean island. – Ecological Research **28**: 317–325.

Kowarik, I. (2011): Novel urban ecosystems, biodiversity, and conservation. – Environmental Pollution **159**: 1974–1983.

Lepczyk, C.A.; Mertig, A.G.; Liu, J. (2004): Landowners and cat predation across rural-to-urban landscapes. – Biological Conservation **115**: 191–201.

Luniak; M. (2004): Synurbization – adaptation of animal wildlife to urban development. – In: Shaw, W.; Harris, L.;Vandruff, L. (eds.): 4th International Urban Wildlife Symposium: 50–55.

MacGregor-Fors, I. (2011): Misconceptions or misunderstandings? On the standardization of basic terms and definitions in urban ecology. – Landscape and Urban Planning **100**: 347–349.

Marzluff, J.M.; Bowman, R.; Donnelly, R.E. (2001): A historical perspective on urban bird research: trends, terms, and approaches. – In: Marzluff, J.M.; Bowman, R. & Donnelly, R.E. (eds.): Avian conservation and ecology in an urbanizing world: 278–282. – Kluwer, New York, USA.

McCleery, R.A. (2009): Changes in fox squirrel antipredator behaviors across the urban rural gradient. – Landscape Ecology **24**: 483–493.

McCleery, R.A.; Lopez, R.R.; Silvy, N.J.; Gallant, D.L. (2009): Fox Squirrel Survival in Urban and Rural Environments. – The Journal of Wildlife Management **72**: 133–137.

McDonnell, M.J.,; Hahs, A.K. (2008): The use of gradient analysis studies in advancing our understanding of the ecology of urbanizing landscapes: current status and future directions. – Landscape Ecology **23**: 1143–1155.

McDonnell, M.J.; Pickett, S.T.A. (1990): Ecosystem structure and function along urban–rural gradients: an unexploited opportunity for ecology. – Ecology **71**: 1232–1237.

Møller, A.P. (2008): Flight distance of urban birds, predation, and selection for urban life. – Behavioral Ecology and Sociobiology **63**: 63–75.

Palomares, F. (2001): Comparison of 3 methods to estimate rabbit abundance in a Mediterranean Environment. – Wildlife Society Bulletin **29**: 578–585.

Partecke, J.; Schwabl, I.; Gwinner, E. (2006): Stress and the City: Urbanization and its effects on the stress physiology in european blackbirds. – Ecology **87**: 1945–1952.

Prange, S.; Gehrt, S.; Wiggers, E. (2003): Demographic Factors Contributing to High Raccoon Densities in Urban Landscapes. – The Journal of Wildlife Management **67**: 324–333.

Robbins, C. (1993): Wildlife feeding and nutrition. – Academic Press, San Diego, California.

Rödel, H.G.; Bora, A.; Kaetzke, P.; Khaschei, M.; Hutzelmeyer, H.; Holst, D. (2004): Over-winter survival in subadult European rabbits: weather effects, density dependence, and the impact of individual characteristics. – Oecologia **140**: 566–576.

Rödel, H.; Dekker, J. (2012): Influence of weather factors on population dynamics of two lagomorph species based on hunting bag records. – European Journal of Wildlife Research **58**: 923–932.

Rogers, P.M.; Myers, K. (1979): Ecology of the European wild rabbit *Oryctolagus cuniculus* (L.) in Mediterranean habitats. I. Distribution in the landscape of the Coto Donana S. Spain. – Journal of Applied Ecology **16**: 691–703.

Schieber, P. (1983): Untersuchungen über Wildkaninchen im Stadtgebiet Münchens. – Dissertation, LMU München.

Smith, A.; Boyer, A. (2008): *Oryctolagus cuniculus*. – In: IUCN 2012. IUCN Red List of Threatened Species. Version 2012.2.

SMITH, T.; ENGEMAN, R. (2002): An extraordinary raccoon, *Procyon lotor*, density at an urban park. – Canadian Field-Naturalist **116**: 636–639.

TARLOW, E.M.; BLUMSTEIN, D.T. (2007): Evaluating methods to quantify anthropogenic stressors on wild animals. – Applied Animal Behaviour Science **102**: 429–451.

VILLAFUERTE, R; MORENO, S. (1997) Predation risk, cover type, and group size in European rabbits in Donana (SW Spain). – Acta Theriologica **42**: 225–230.

WERNER; P. (2011): The ecology of urban areas and their functions for species diversity. – Landscape and Ecological Engineering **7**: 231–240.

WESSOLEK; E.M. (2008): Sealing of Soils. – In: MARZLUFF, J.M. et al. (eds.): Urban Ecology An International Perspective on the Interaction Between Humans and Nature 161–180.

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Chapter 3

Effects of urbanization on burrow characteristics and group sizes.

This chapter consists of the following publication:

Ziege M, Brix M, Schulze M, Seidemann A, Straskraba S, Wenninger S, Streit B, Wronski T & Plath M (2015). From multifamily residences to studio apartments: shifts in burrow structures of European rabbits along a rural-to-urban gradient. Journal of Zoology, 295:286-293.

Ziege, Brix, Wenninger and Plath designed the theoretical framework. Ziege, Brix, Schulze, Seidemann, Straskraba and Wenninger collected and analyzed data. Ziege, Streit, Wronski and Plath wrote and corrected the manuscript. More details on contributions of me and my co-authors are given below in the form "Anlage 1: Ausführungsbestimmungen für Dissertationen im Promotionsfach Biologie, die bereits veröffentlichte Teile oder eingereichte Manuskripte enthalten".

Anlage 1

Erklärung zu den Autorenanteilen

an der Publikation / des Manuskripts (Titel):

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

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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 min^{-1} 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):

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

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):

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

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).

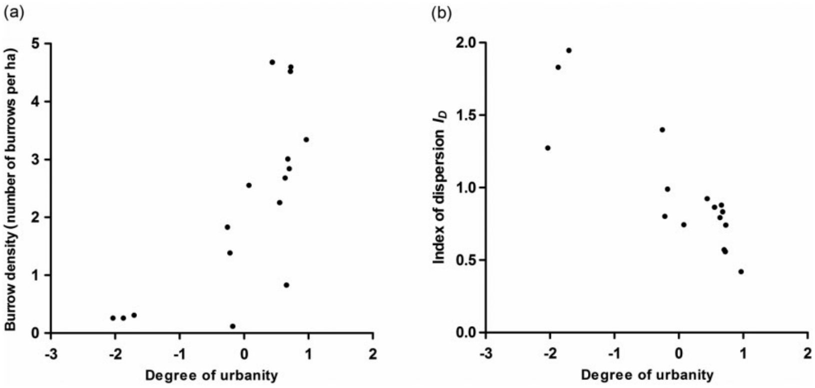

Figure 1 Correlation between the 'degree of urbanity' and (a) numbers of rabbit burrows per ha and (b) the index of dispersion (I_D).

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

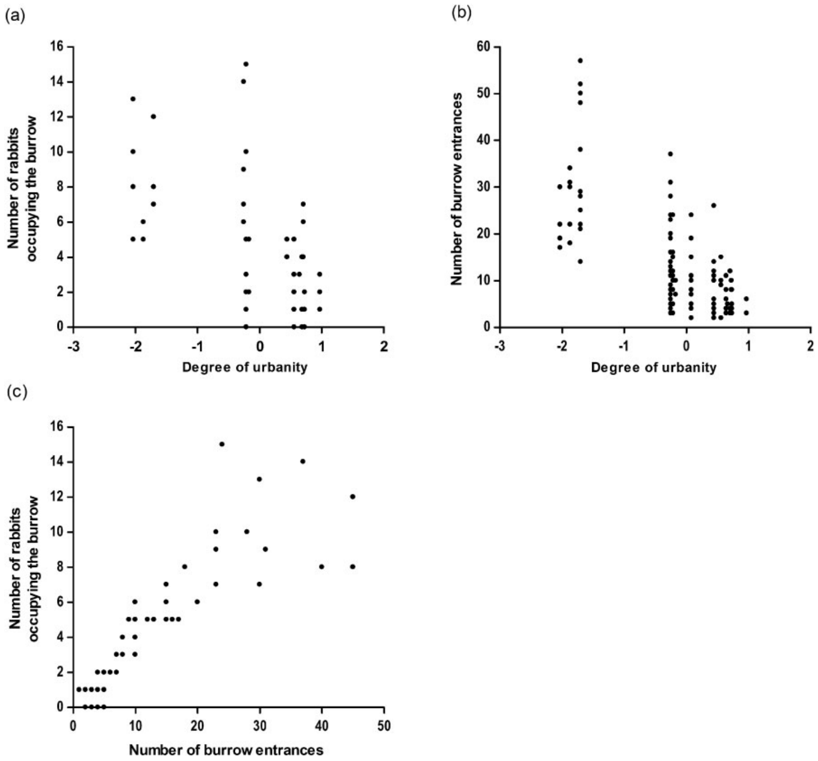

Figure 2 Correlation between the 'degree of urbanity' and (a) numbers of rabbits inhabiting a burrow and (b) numbers of burrow entrances. (c) Correlation between numbers of burrow entrances and numbers of rabbits inhabiting the same burrow system.

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

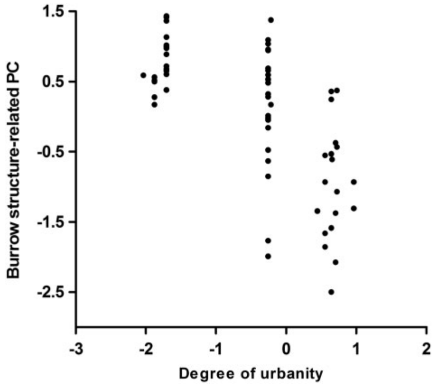

Figure 3 Correlation between the 'degree of urbanity' and the burrow structure-related PC (for details, see main text).

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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References

Adams, L.W. (1994). *Urban wildlife habitats: a landscape perspective*. Vol. 3. Minneapolis: University of Minnesota Press.

Adkins, C.A. & Stott, P. (1998). Home ranges, movements and habitat associations of red foxes *Vulpes vulpes* in suburban Toronto, Ontario, Canada. *J. Zool. (Lond.)* **244**, 335–346.

Alberti, M., Botsford, E. & Cohen, A. (2001). Quantifying the urban gradient: linking urban planning and ecology. In *Avian ecology and conservation in an urbanizing world*: 89–115. Marzluff, J.M., Bowman, R. & Donnelly, R. (Eds). Norwell: Kluwer Academic Publishers.

Alberti, M., Marzluff, J.M., Shulenberger, E., Bradley, G., Ryan, C. & Zumbrunnen, C. (2008). Integrating humans into ecology: opportunities and challenges for studying urban ecosystems. In *Urban ecology*: 143–158. Marzluff, J.M., Shulenberger, E., Endlicher, W., Alberti, M., Bradley, G., Ryan, C., Simon, U. & ZumBrunnen, C. (Eds). New York: Springer.

Angulo, E. & Villafuerte, R. (2004). Modelling hunting strategies for the conservation of wild rabbit populations. *Biol. Conserv.* **115**, 291–301.

Armour, C.J. & Thompson, H.V. (1955). Spread of myxomatosis in the first outbreak in Great Britain. *Ann. Appl. Biol.* **43**, 511–518.

Arnold, J.M., Greiser, G., Keuling, O., Martin, I. & Straus, E. (2013). *Status und Entwicklung ausgewählter Wildtierarten in Deutschland. Jahresbericht 2012. Wildtier-Informationssystem der Länder Deutschlands (WILD)*. Hg. v. Dtsch. Jagdverband e.V., Berlin

Arnold, W. (1988). Social thermoregulation during hibernation in alpine marmots (*Marmota marmota*). *J. Comp. Physiol. [B.]* **158**, 151–156.

Baker, P.J. & Harris, S. (2007). Urban mammals: what does the future hold? An analysis of the factors affecting patterns of use of residential gardens in Great Britain. *Mamm. Rev.* **37**, 297–315.

Bell, D.J. (1983). Mate choice in the European rabbit. In *Mate choice*: 211–223. Bateson, P.P.G. (Ed.). Cambridge: Cambridge University Press.

Calvete, C., Estrada, R., Angulo, E. & Cabezas-Ruiz, S. (2004). Habitat factors related to wild rabbit conservation in an agricultural landscape. *Landsc. Ecol.* **19**, 531–542.

Cowan, D.P. (1984). The use of ferrets (*Mustela furo*) in the study and management of the European wild rabbit (*Oryctolagus cuniculus*). *J. Zool. (Lond.)* **204**, 570–574.

Cowan, D.P. (1987). Group living in the European rabbit (*Oryctolagus cuniculus*): mutual benefit or resource localization? *J. Anim. Ecol.* **56**, 779–795.

Davison, J., Huck, M., Delahay, R.J. & Roper, T.J. (2008). Urban badger setts: characteristics, patterns of use and management implications. *J. Zool. (Lond.)* **275**, 190–200.

Davison, J., Huck, M., Delahay, R.J. & Roper, T.J. (2009). Restricted ranging behaviour in a high-density population of urban badgers. *J. Zool. (Lond.)* **277**, 45–53.

Delibes-Mateos, M., Farfán, M.Á., Olivero, J. & Vargas, J.M. (2010). Land-use changes as a critical factor for long-term wild rabbit conservation in the Iberian Peninsula. *Environ. Conserv.* **37**, 169–176.

Ditchkoff, S.S., Saalfeld, S.T. & Gibson, C.J. (2006). Animal behavior in urban ecosystems: modifications due to human-induced stress. *Urban Ecosyst.* **9**, 5–12.

Ferreira, C., Touza, J., Rouco, C., Díaz-Ruiz, F., Fernandez-de-Simon, J., Ríos-Saldaña, C.A., Ferreras, P., Villafuerte, R. & Delibes-Mateos, M. (2014). Habitat management as a generalized tool to boost European rabbit *Oryctolagus cuniculus* populations in the Iberian Peninsula: a cost-effectiveness analysis. *Mamm. Rev.* **44**, 30–43.

Fischer, J.D., Cleeton, S.H., Lyons, T.P. & Miller, J.R. (2012). Urbanization and the predation paradox: the role of trophic dynamics in structuring vertebrate communities. *Bioscience* **62**, 809–818.

Fleming, M.R. (1980). Thermoregulation and torpor in the sugar glider, *Petaurus breviceps* (Marsupialia: Petauridae). *Aust. J. Zool.* **28**, 521–534.

Gea-Izquierdo, G., Muñoz-Igualada, J. & San Miguel-Ayanz, A. (2005). Rabbit warren distribution in relation to pasture communities in Mediterranean habitats: consequences for management of rabbit populations. *Wildl. Res.* **32**, 723–731.

Gering, J.C. & Blair, R.B. (1999). Predation on artificial bird nests along an urban gradient: predatory risk or relaxation in urban environments? *Ecography* **22**, 532–541.

Guerrero-Casado, J., Carpio, A.J., Ruiz-Aizpurua, L. & Tortosa, F.S. (2013). Restocking a keystone species in a biodiversity hotspot: recovering the European rabbit on a landscape scale. *J. Nat. Conserv.* **21**, 444–448.

Harper, S.J. & Batzli, G.O. (1996). Effects of predators on structure of the burrows of voles. *J. Mammal.* **77**, 1114–1121.

IUCN (2014). *The IUCN red list of threatened species*. Version 2014.3.<www.iucnredlist.org>. Downloaded on 25 December 2014.

Jokimäki, J. & Huhta, E. (2000). Artificial nest predation and abundance of birds along an urban gradient. *The Condor* **102**, 838–847.

Kolb, H.H. (1985). The burrow structure of the European rabbit (*Oryctolagus cuniculus* L.). *J. Zool. (Lond.)* **206**, 253–262.

Kowarik, I. (2011). Novel urban ecosystems, biodiversity, and conservation. *Environ. Pollut.* **159**, 1974–1983.

Krebs, C.J. (1999). *Ecological methodology*. 2nd edn. Menlo Park: Addison Wesley, Longman Inc.

Lees, A.C. & Bell, D.J. (2008). A conservation paradox for the 21st century: the European wild rabbit *Oryctolagus cuniculus*, an invasive alien and an endangered native species. *Mamm. Rev.* **38**, 304–320.

Lombardi, L., Fernández, N., Moreno, S. & Villafuerte, R. (2003). Habitat-related differences in rabbit (*Oryctolagus cuniculus*) abundance, distribution, and activity. *J. Mammal.* **84**, 26–36.

McKinney, M.L. (2002). Urbanization, biodiversity, and conservation. *Bioscience* **52**, 883–890.

McKinney, M.L. (2006). Urbanization as a major cause of biotic homogenization. *Biol. Conserv.* **127**, 247–260.

McKinney, M.L. (2008). Effects of urbanization on species richness: a review of plants and animals. *Urban Ecosyst.* **11**, 161–176.

Moreno, S. & Villafuerte, R. (1995). Traditional management of scrubland for the conservation of rabbits *Oryctolagus cuniculus* and their predators in Doñana National Park, Spain. *Biol. Conserv.* **73**, 81–85.

Møller, A.P. (2008). Flight distance of urban birds, predation, and selection for urban life. *Behav. Ecol. Sociobiol.* **63**, 63–75.

Palomares, F. (2003). Warren building by European rabbits (*Oryctolagus cuniculus*) in relation to cover availability in a sandy area. *J. Zool. (Lond.)* **259**, 63–67.

Pickett, S.T.A., Cadenasso, M.L., Grove, J.M., Nilon, C.J., Pouyat, R. V, Zipperer, W.C. & Costanza, R. (2001). Urban ecological systems: linking terrestrial ecological, physical, and socioeconomic components of metropolitan areas. *Annu. Rev. Ecol. Syst.* **32**, 127–157.

Prange, S., Gehrt, S.D. & Wiggers, E.P. (2003). Demographic factors contributing to high raccoon densities in urban landscapes. *J. Wildl. Mgmt.* **67**, 324–333.

Roper, T.J. (1992). Badger *Meles meles* setts – architecture, internal environment and function. *Mamm. Rev.* **22**, 43–53.

Shochat, E. (2004). Credit or debit? Resource input changes population dynamics of city-slicker birds. *Oikos* **106**, 622–626.

Shochat, E., Warren, P.S., Faeth, S.H., McIntyre, N.E. & Hope, D. (2006). From patterns to emerging processes in mechanistic urban ecology. *Trends Ecol. Evol.* **21**, 186–191.

Villafuerte, R. & Moreno, S. (1997). Predation risk, cover type, and group size in European rabbits in Doñana (SW Spain). *Acta Theriol.* **42**, 225–230.

Villafuerte, R., Calvete, C., Blanco, J.C. & Lucientes, J. (1995). Incidence of viral hemorrhagic disease in wild rabbit populations in Spain. *Mammalia* **59**, 651–659.

Ziege, M., Babitsch, D., Brix, M., Kriesten, S., Seidemann, A., Wenninger, S. & Plath, M. (2013). Anpassungsfähigkeit des Europäischen Wildkaninchens entlang eines rural-urbanen Gradienten. *Beiträge zur Jagd- und Wildtierforsch.* **38**, 189–199.

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).

Chapter 4

Effects of urbanization on activity patterns and time budgets.

This chapter consists of the following publication:

Ziege M, Babitsch D, Brix M, Kriesten S, Straskraba S, Wenninger S, Wronski T & Plath M (2016a). Extended diurnal activity patterns of European rabbits along a rural-to-urban gradient. *Mammalian Biology - Zeitschrift für Säugetierkunde*, 81:534-541.

Ziege, Brix, Wronski and Plath designed the theoretical framework, wrote and corrected the manuscript. Ziege, Babitsch, Brix, Kriesten, Straskraba and Wenninger collected and analyzed data. More details on contributions of me and my co-authors are given below in the form "Anlage 1: Ausführungsbestimmungen für Dissertationen im Promotionsfach Biologie, die bereits veröffentlichte Teile oder eingereichte Manuskripte enthalten".

Anlage 1

Erklärung zu den Autorenanteilen

an der Publikation / des Manuskripts (Titel):

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Unterschrift Betreuer: ____________________Datum/Ort: Frankfurt a.M., 14.11.2016_____

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Original investigation

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

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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

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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-

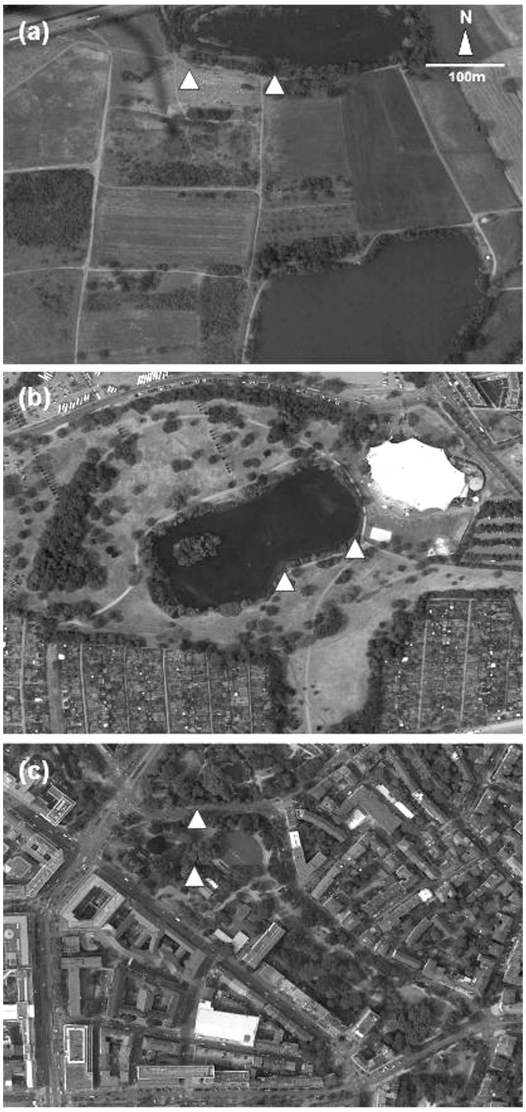

Fig. 1. Study sites.
(a) One of our rural study sites at Maintal, (b) suburban site Rebstockpark, and (c) urban study site no 1. White triangles indicate focal burrows within study sites.
Source: Google Earth.

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; Fig. 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 hindfeet; *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 × 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 × 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 × 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 ± SE = 21.8 ± 1.4%, $n = 384$ focal scans). High values of 18.0 ± 1.3% ($n = 390$ focal scans) were also found at urban study sites, while only 12.2 ± 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 × 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

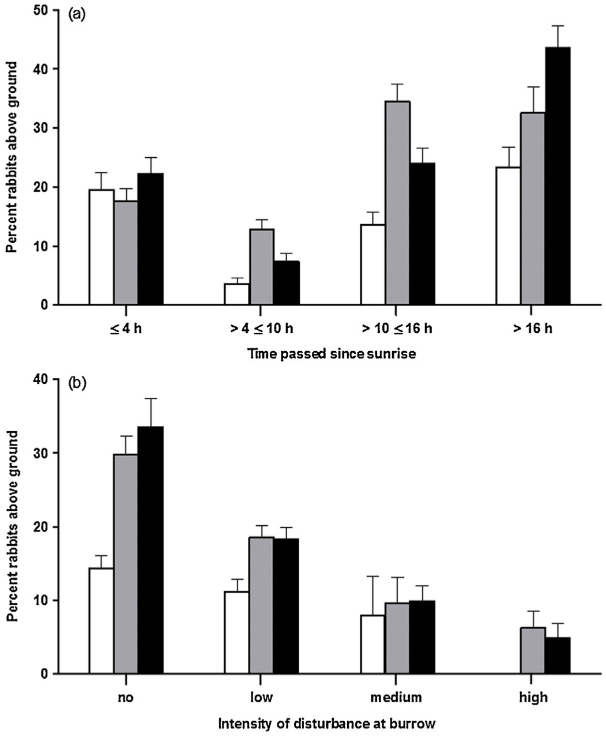

Fig. 2. Activity above ground.
Mean (±SE) percentage of rabbits above ground at rural (white), suburban (grey) and urban (black) sites with respect to (a) the time passed since sunrise and (b) different intensities of disturbance at the focal burrows (low disturbance: between 1 and 5 persons/dogs within 50 m around the burrow, medium disturbance: between 5 and 10 persons/dogs, high disturbance: >10 persons/dogs).

Table 3
Mean (±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 ± 2.5	18.9 ± 2.1	22.6 ± 2.1
Grazing	40.5 ± 3.2	54.4 ± 2.8	45.6 ± 2.6
Moving	6.7 ± 1.4	6.9 ± 1.2	12.6 ± 1.2
Resting	9.4 ± 2.4	15.5 ± 2.0	15.7 ± 2.1
Socio-positive interactions	0.8 ± 0.3	0.5 ± 0.2	0.3 ± 0.2
Socio-negative interactions	0.4 ± 0.4	0.6 ± 0.2	0.6 ± 0.2
Others	2.8 ± 1.0	3.2 ± 0.8	2.6 ± 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 ± 1.8% of the rabbits per burrow were observed above ground at rural study sites, while urban (33.5 ± 3.2%) and suburban (29.8 ± 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 between data-sets from suburban and urban sites (Tables 3 and 4; Fig. 3).

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 × 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		

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 ± SE for fastest reappearance times at the rural study site: 1st = 336 ± 128 s, 2nd = 174 ± 99 s, 3rd = 147 ± 41 s, 4th = 255 ± 60 s, 5th = 196 ± 85 s; suburban study site: 1st = 478 ± 128 s, 2nd = 367 ± 99 s, 3rd = 88 ± 41 s, 4th = 141 ± 60 s, 5th = 265 ± 85 s). We found no significant effect of the interaction term 'repeated measures × urbanity' and no main effect of 'urbanity' (Table 5).

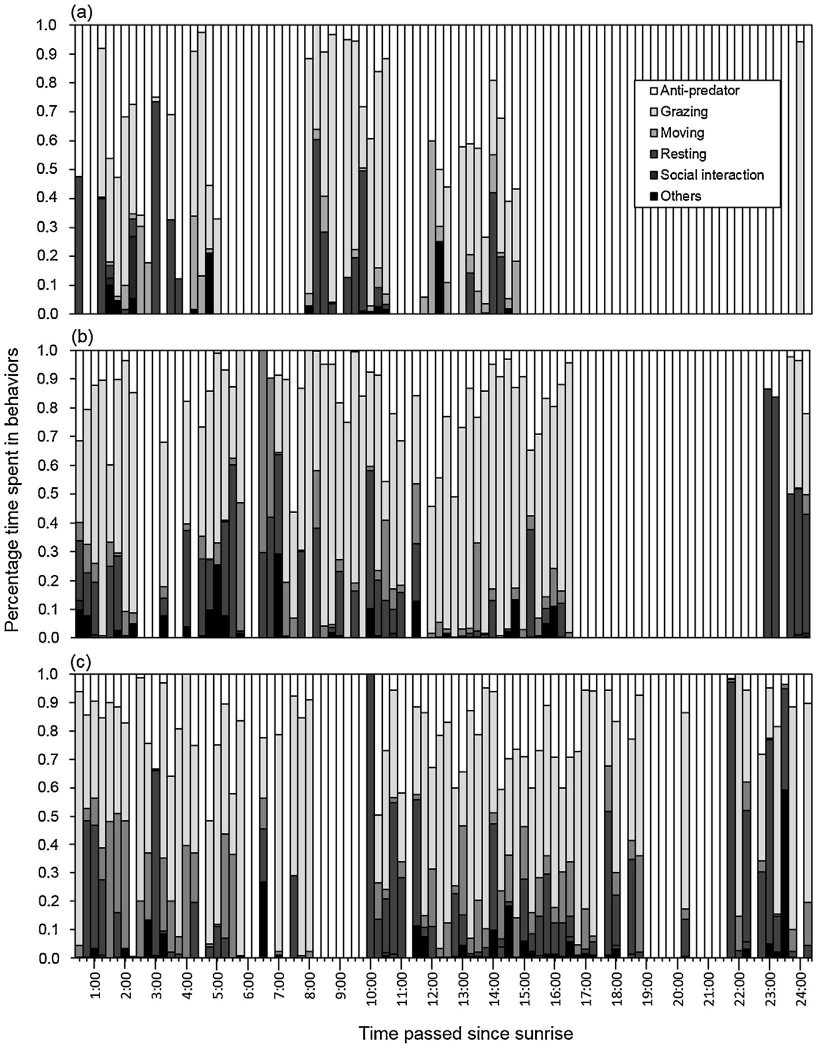

Fig. 3. Time budgets.
Time budgets of rabbits at (a) rural, (b) suburban, and (c) urban study sites in and around Frankfurt a.M. in Germany. Shown are percentage proportions of anti-predator behaviors (including time spent inside burrows), grazing, moving, resting, social interactions and other behaviors (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 then 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 would 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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References

Adams, R.A., Lengas, B.J., Bekoff, M., 1987. Variations in avoidance responses to humans by black-tailed prairie dogs (*Cynomys ludovicianus*). J. Mammal. 68, 686–689.

Arnold, J.M., Greiser, G., Keuling, O., Martin, I., Straus, E., 2013. Status und Entwicklung ausgewählter Wildtierarten in Deutschland. Jahresbericht 2012. Wildtier-Informationssystem der Länder Deutschlands (WILD), (Ed.) Deutscher Jagdverband e.V.

Baker, P.J., Molony, S.E., Stone, E., Cuthill, I.C., Harris, S., 2008. Cats about town: is predation by free-ranging pet cats *Felis catus* likely to affect urban bird populations? Ibis 150, 86–99.

Bateman, P.W., Fleming, P.A., 2014. Does human pedestrian behaviour influence risk assessment in a successful mammal urban adapter? J. Zool. 294, 93–98.

Blumstein, D.T., Evans, C.S.E., Daniels, J.C., 2006. JWatcher 1.0. http://www.jwatcher.ucla.Edu.

Brivio, F., Bertolucci, C., Tettamanti, F., Filli, F., Apollonio, M., Grignolio, S., 2016. The weather dictates the rhythms: Alpine chamois activity is well adapted to ecological conditions. Behav. Ecol. Sociobiol. 70, 1291–1304.

Chapman, T., Rymer, T., Pillay, N., 2012. Behavioural correlates of urbanisation in the Cape ground squirrel *Xerus inauris*. Naturwissenschaften 99, 893–902.

Contesse, P., Hegglin, D., Gloor, S., Bontadina, F., Deplazes, P., 2004. The diet of urban foxes (*Vulpes vulpes*) and the availability of anthropogenic food in the city of Zurich, Switzerland. Mamm. Biol. 69, 81–95.

Ditchkoff, S.S., Saalfeld, S.T., Gibson, C.J., 2006. Animal behavior in urban ecosystems: modifications due to human-induced stress. Urban Ecosyst. 9, 5–12.

Duduś, L., Zalewski, A., Kozioł, O., Jakubiec, Z., Król, N., 2014. Habitat selection by two predators in an urban area: the stone marten and red fox in Wrocław (SW Poland). Mamm. Biol. 79, 71–76.

Estes, W., Mannan, R., 2003. Feeding behavior of Cooper's hawks at urban and rural nests in southeastern Arizona. Condor 105, 107–116.

Evans, K.L., Gaston, K.J., Frantz, A.C., Simeoni, M., Sharp, S.P., McGowan, A., Dawson, D.A., Walasz, K., Partecke, J., Burke, T., Hatchwell, B.J., 2009. Independent colonization of multiple urban centres by a formerly forest specialist bird species. Proc. R. Soc. Lond. B 276, 2403–2410.

Evans, J., Boudreau, K., Hyman, J., 2010. Behavioural syndromes in urban and rural populations of song sparrows. Ethology 116, 588–595.

Ferreira, C., Touza, J., Rouco, C., Díaz-Ruiz, F., Fernandez-de-Simon, J., Ríos-Saldaña, C.A., Ferreras, P., Villafuerte, R., Delibes-Mateos, M., 2014. Habitat management as a generalized tool to boost European rabbit *Oryctolagus cuniculus* populations in the Iberian Peninsula: a cost-effectiveness analysis. Mamm. Rev. 44, 30–43.

French, S.S., Fokidis, H.B., Moore, M.C., 2008. Variation in stress and innate immunity in the tree lizard (*Urosaurus ornatus*) across an urban-rural gradient. J. Comp. Physiol. B 178, 997–1005.

Frid, A., Dill, L., 2002. Human-caused disturbance stimuli as a form of predation risk. Conserv. Ecol. 6, 1.

Gibb, J.A., 1993. Sociality, time and space in a sparse population of rabbits (*Oryctolagus cuniculus*). J. Zool. (Lond.) 229, 581–607.

Gloor, S., Bontadina, F., Hegglin, D., Deplazes, P., Breitenmoser, U., 2001. The rise of urban fox populations in Switzerland. Mamm. Biol. 66, 155–164.

Harris, S., Baker, P.J., Soulsbury, C.D., Iossa, G., 2010. Eurasian badger (*Meles meles*). In: Gehrt, S.D., Riley, S.P.D., Cypher, B.L. (Eds.), Urban Carnivores: Ecology, Conflict, and Conservation. Johns Hopkins University Press, Baltimore.

Iossa, G., Soulsbury, C.D., Baker, P.J., Harri, S., 2010. A taxonomic analysis of urban carnivore ecology: coyotes (*Canis latrans*). In: Gehrt, S., Riley, S., Cypher, B. (Eds.), Urban Carnivores: Ecology, Conflict, and Conservation. Johns Hopkins University Press, Baltimore, pp. 173–180.

Kremer, M., 1993. Population growth and technological change: one million B.C. to 1990. J. Econ. 108, 681–716.

Kübler, S., Kupko, S., Zeller, U., 2005. The kestrel (*Falco tinnunculus* L.) in Berlin: investigation of breeding biology and feeding ecology. J. Ornithol. 146, 271–278.

Lehrer, E.W., Schooley, R.L., Whittington, J.K., 2011. Survival and antipredator behavior of woodchucks (*Marmota monax*) along an urban–agricultural gradient. Can. J. Zool. 90, 12–21.

Lombardi, L., Fernández, N., Moreno, S., Villafuerte, R., 2003. Habitat-related differences in rabbit (*Oryctolagus cuniculus*) abundance, distribution, and activity. J. Mammal. 84, 26–36.

Lombardi, L., Fernández, N., Moreno, S., Fernández, N., 2007. Habitat use and spatial behaviour in the European rabbit in three Mediterranean environments. Basic Appl. Ecol. 8, 453–463.

Møller, A.P., Diaz, M., Flensted-Jensen, E., Grim, T., Ibáñez-Álamo, J.D., Jokimäki, J., Mänd, R., Markó, G., Tryjanowski, P., 2012. High urban population density of birds reflects their timing of urbanization. Oecologia 170, 867–875.

Møller, A.P., 2008. Flight distance of urban birds, predation, and selection for urban life. Behav. Ecol. Sociobiol. 63, 63–75.

Møller, A.P., 2012. Urban areas as refuges from predators and flight distance of prey. Behav. Ecol. 23, 1030–1035.

Magle, S.B., Angeloni, L.M., 2011. Effects of urbanization on the behaviour of a keystone species. Behaviour 148, 31–54.

Martin, P., Bateson, P., 1986. Measuring Behaviour. Cambridge University Press, New York.

McCleery, R.A., Lopez, R.R., Silvy, N.J., Gallant, D.L., 2008. Fox squirrel survival in urban and rural environments. J. Wildl. Manag. 72, 133–137.

McCleery, R.A., 2009. Changes in fox squirrel anti-predator behaviors across the urban rural gradient. Landsc. Ecol. 24, 483–493.

McKinney, M.L., 2008. Effects of urbanization on species richness: a review of plants and animals. Urban Ecosyst. 11, 161–176.

Moreno, S., Beltrán, J.F., Cotilla, I., Kuffner, B., Laffite, R., Jordán Ayala, J., Quintero, C., Jiménez, A., Castro, F., Cabezas, S., Villafuerte, R., 2008. Long-term decline of the European wild rabbit (*Oryctolagus cuniculus*) in south-western Spain. Wildl. Res. 34, 652–658.

Moseby, K.E., De Jong, S., Munro, N., Pieck, A., 2005. Home range, activity and habitat use of European rabbits (*Oryctolagus cuniculus*) in arid Australia: implications for control. Wildl. Res. 32, 305–311.

Partecke, J., Schwabl, I., Gwinner, E., Rhythms, B., 2006. Stress and the city: urbanization and its effects on the stress physiology in European blackbirds. Ecology 87, 1945–1952.

Pickett, S.T.A., Cadenasso, M.L., Grove, J.M., Nilon, C.J., Pouyat, R.V., Zipperer, W.C., Costanza, R., 2001. Urban ecological systems: linking terrestrial, ecological, physical, and socioeconomic components of metropolitan areas. Annu. Rev. Ecol. Syst. 32, 127–157.

Pickett, S.T.A., Cadenasso, M.L., Grove, J.M., Nilon, C.H., Pouyat, R.V., Zipperer, W.C., Constanza, R., 2008. Urban ecological systems: linking terrestrial ecological, physical, and socioeconomic components of metropolitan areas. In: Urban Ecology. Springer, US, pp. 99–122.

Prange, S., Gehrt, S.D., Wiggers, E.P., 2003. Demographic factors contributing to high raccoon densities in urban landscapes. J. Wildl. Manag. 67, 324–333.

Ramalho, C.E., Hobbs, R.J., 2012. Time for a change: dynamic urban ecology. Trends Ecol. Evol. 27, 179–188.

Riley, S.P.D., Sauvajot, R.M., Fuller, T.K., York, E.C., Kamradt, D.A., Bromley, C., Wayne, R.K., 2003. Effects of urbanization and habitat fragmentation on bobcats and coyotes in southern California. Conserv. Biol. 17, 566–576.

Risch, M., Dwenger, A., Wirth, H., 1996. Der Sperber (*Accipiter nisus*) als Brutvogel in Hamburg: Bestandsentwicklung und Bruterfolg 1982–1996. Hamburger Avifauna 28, 43–57.

Rodewald, A.D., Gehrt, S.D., 2014. Wildlife population dynamics in urban landscapes. In: McCleery, R.A., Moorman, C.E., Peterson, M.N. (Eds.), Urban Wildlife Conservation—Theory and Praxis. Springer, New York, pp. 117–147.

Rosenfield, R.N., Bielefeldt, J., Affeldt, J.L., Beckmann, D.J., 1995. Nesting density, nest area reoccupancy, and monitoring implications for Cooper's hawks in Wisconsin. J. Raptor Res. 29, 1–4.

Rutz, C., 2006. Home range size, habitat use, activity patterns and hunting behaviour of urban-breeding Northern Goshawks *Accipiter gentilis*. Ardea 94, 185–202.

Ryan, A.M., Partan, S.R., 2014. Urban wildlife behavior. In: McCleery, R.A., Moorman, C.E., Peterson, N.M. (Eds.), Urban Wildlife Conservation—Theory and Praxis. Springer, New York, pp. 149–173.

Shochat, E., Warren, P.S., Faeth, S.H., McIntyre, N.E., Hope, D., 2006. From patterns to emerging processes in mechanistic urban ecology. Trends Ecol. Evol. 21, 186–191.

Smith, A.T., Boyer, A.F., 2008. *Oryctolagus cuniculus*, in: IUCN 2013. IUCN Red List of Threatened Species.

United Nations Population Division, 2014. World Urbanization Prospects: The 2014 Revision. New York, accessed 24.12.15 http://esa.un.org/unpd/wup/CD-Rom/Urban-Rural-Population.htm.

Virgós, E., Cabezas-Díaz, S., Malo, A., Lozano, J., López-Huertas, D., 2003. Factors shaping European rabbit abundance in continuous and fragmented populations of central Spain. Acta Theriol. (Warsz) 48, 113–122.

von Holst, D., Hutzelmeyer, H., Kaetzke, P., Khaschei, M., Schönheiter, R., 1999. Social rank, stress, fitness, and life expectancy in wild rabbits. Naturwissenschaften 86, 388–393.

Vosburgh, T.C., Irby, L.R., 1998. Effects of recreational shooting on prairie dog colonies. J. Wildl. Manag. 62, 363–372.

Ziege, M., Babitsch, D., Brix, M., Kriesten, S., Seidemann, A., Wenninger, S., Plath, M., 2013. Anpassungsfähigkeit des Europäischen Wildkaninchens entlang eines rural-urbanen Gradienten. Beiträge zur Jagd- und Wildtierforsch. 38, 189–199.

Ziege, M., Brix, M., Schulze, M., Seidemann, A., Straskraba, S., Wenninger, S., Streit, B., Wronski, T., Plath, M., 2015. From multifamily residences to studio apartments—shifts in burrow structures of European rabbits along a rural-to-urban gradient. J. Zool. 295, 286–293.

Ziege, M., Bierbach, D., Bischoff, S., Brandt, A.-L., Brix, M., Greshake, B., Merker, S., Wenninger, S., Wronski, T., Plath, M., 2016. Importance of latrine communication in European rabbits shifts along a rural-to-urban gradient. BMC Ecol., e16–e29.

Chapter 5

Effects of urbanization on communication behaviors (latrine-based marking networks).

This chapter consists of the following publication:

Ziege M, Bierbach D, Bischoff S, Brandt AL, Brix M, Greshake B, Merker S, Wenninger S, Wronski T & Plath M (2016b). Importance of latrine communication in European rabbits shifts along a rural-to-urban gradient. *BMC Ecology*, 16:29.

Ziege, Brix, Merker, Wronski and Plath designed the theoretical framework. Ziege, Bierbach, Bischoff, Brandt, Brix, Greshake and Wenninger collected and analyzed data. Ziege, Merker, Wronski and Plath wrote and corrected the manuscript. More details on contributions of me and my co-authors are given below in the form "Anlage 1: Ausführungsbestimmungen für Dissertationen im Promotionsfach Biologie, die bereits veröffentlichte Teile oder eingereichte Manuskripte enthalten".

Anlage 1

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BMC Ecology

RESEARCH ARTICLE

Importance of latrine communication in European rabbits shifts along a rural–to–urban gradient

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Abstract

Background: Information transfer in mammalian communication networks is often based on the deposition of excreta in latrines. Depending on the intended receiver(s), latrines are either formed at territorial boundaries (*between-group communication*) or in core areas of home ranges (*within-group communication*). The relative importance of both types of marking behavior should depend, amongst other factors, on population densities and social group sizes, which tend to differ between urban and rural wildlife populations. Our study is the first to assess (direct and indirect) anthropogenic influences on mammalian latrine-based communication networks along a rural-to-urban gradient in European rabbits (*Oryctolagus cuniculus*) living in urban, suburban and rural areas in and around Frankfurt am Main (Germany).

Results: The proportion of latrines located in close proximity to the burrow was higher at rural study sites compared to urban and suburban ones. At rural sites, we found the largest latrines and highest latrine densities close to the burrow, suggesting that core marking prevailed. By contrast, latrine dimensions and densities increased with increasing distance from the burrow in urban and suburban populations, suggesting a higher importance of peripheral marking.

Conclusions: Increased population densities, but smaller social group sizes in urban rabbit populations may lead to an increased importance of *between-group communication* and thus, favor peripheral over core marking. Our study provides novel insights into the manifold ways by which man-made habitat alterations along a rural-to-urban gradient directly and indirectly affect wildlife populations, including latrine-based communication networks.

Keywords: Chemical communication, Communication center, Core marking, Localized defecation, Urban ecology

Background

Mammalian communication through localized defecation sites

The transmission of information in localized defecation sites (latrines) plays a central role in mammalian communication ([1–3], reviewed in [4]). Latrines deposited along territory boundaries are known to serve as a visual and olfactory fence, not only to indicate territorial occupancy, but also to signal the competitive ability of the territory owner(s), e.g., towards neighboring territory holders (*between-group communication*; seen in European badgers, *Meles meles* [5, 6]; lemurs [7]; meerkats, *Suricata suricatta* [8], and bushbuck, *Tragelaphus scriptus* [9]). Besides this peripheral marking behavior, several species also establish latrines in central parts of their home ranges—termed core marking—in order to support the monopolization of key resources, such as food, shelter, burrows, or nest sites (seen in European badgers [6, 10], lemurs [4, 7], and Arabian gazelles, *Gazella arabica* [11, 12]). Furthermore, latrines that are located in core areas of home ranges facilitate information exchange between the members of the same social group and thus, can enhance and maintain social bonds or dominance hierarchies (*within-group communication* [6, 13, 14]).

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Relative importance of core vs. peripheral marking behavior

Dröscher and Kappeler [4] recently highlighted that we still have a limited understanding about how different ecological factors influence the structure and complexity of mammalian latrine-based communication networks. The relative importance of core vs. peripheral marking behavior seems to depend on population ecological variables; e.g., higher population densities increase competition for territorial space and thus, the necessity to indicate territorial occupancy. This, in turn, favors peripheral over core marking, as suggested for high density rural European badger populations [15, 16] (for European rabbits, *Oryctolagus cuniculus*, see also [17]).

Furthermore, economic considerations predict that the establishment, use, and maintenance of latrines depends on the time and energy animals can effectively invest in their marking behavior [3, 18]. If territory dimensions exceed a certain size, peripheral marking is likely to be replaced by the less time-consuming core marking behavior [3, 4, 18]. Likewise, if the number of individuals that contribute to peripheral marking is low and/or animals need to allocate a considerable proportion of their time to other behaviors—e.g., because they spend more time avoiding predators or human disturbance—latrine distribution patterns should become less complex, and a shift towards core marking would be predicted.

Effects of urbanization on latrine-based communication networks

Population densities of some mammalian species are higher in urban habitats compared to rural areas ([19–21], reviewed in [22]). Moreover, changes in population densities can be accompanied by differences in social organization, such as smaller social group sizes (European rabbits: [23]) or a less coherent social organization in urban and suburban populations (European badgers: [24–26]). Typical behavioral changes in some urban populations include a reduction in time spent foraging [27] and reduced territorial behavior [24–26], along with smaller territory dimensions (e.g., in raccoons, *Procyon lotor* [27]; European badgers [26]; or red foxes, *Vulpes vulpes* [28]; reviewed in [29]). While the aforementioned species are crepuscular and avoid human disturbance [5, 30], other species, like European rabbits, show extended activity rhythms and reduced anti-predator behavior in urban regions [31, 32], and so they are also unlikely to reduce territorial behavior.

Empirical studies considering the question of how urbanization affects latrine-based communication networks are largely restricted to European badgers [25, 26]. In rural areas, where badgers reached high population densities, both core—("hinterland marking" [5, 6, 10]) and peripheral marking behaviors were reported, but peripheral marking prevailed [15, 16]. Specifically, peripheral latrines were larger, more densely packed, and showed higher utilization frequencies [16]. By contrast, no peripheral latrines were found in a low-density suburban badger population in Bristol [25] and a high-density urban population in Brighton [26]. In case of the Bristol population, latrines accumulated close to the burrow, suggesting a role of latrines for communication within groups. A recent study by Domínguez-Cebrían and de Miguel [33] investigated the latrine-based communication network of a European rabbit population in a suburban forest of Madrid. Latrines deposited at the territorial periphery were previously hypothesized to signal territory occupancy in rabbits, whereas latrines situated in proximity to the burrow likely facilitate information exchange among group members [13, 14, 34–38]. Domínguez-Cebrían and de Miguel [33] found numbers of latrines to decrease with increasing distance from the burrow system and discuss that rabbits could face a higher predation risk when using peripheral latrines. However, no information was provided by the authors on population densities or social group sizes that would have allowed conclusions regarding the question of how (direct and indirect) effects of urbanization influence latrine-based communication networks in their study population.

Objectives of this study

European rabbits exchange information about individuals' age, sex, reproductive condition, and social status via secretions emanating from the anal and submandibular glands [14, 38, 39]. Rabbits deposit hard fecal pellets at latrines that are covered with anal gland secretions [36, 40] and smear secretions from the submandibular gland onto fecal pellets during so-called "chinning" behavior [14, 37, 39, 40]. It is thus well conceivable that latrines at territorial boundaries provide information about territorial occupancy to potential territory intruders (*between-group communication*) (e.g., [13, 14, 34–38]). In contrast, the common use of latrines located at core areas by different members of the same social rabbit group is probably mainly related to the establishment and maintenance of social group structures (*within-group communication*) [13, 14]. Previous studies were suggestive of a pattern in which peripheral marking is pronounced when population densities are high and distinct social groups are competing ([17], see also [15, 16] for European badger populations).

Population densities of European rabbits in rural areas of Europe are currently on decline [31, 41–44], while at the same time rabbits can reach high densities in urban and suburban areas (for Germany see [31, 43]) but tend to form much smaller social groups [23]. This trend is probably largely caused by intensified agricultural practices in rural areas, where the availability, e.g., of thickets for burrow construction is decreasing [23, 41–44]. Hence, European rabbits are an interesting species to compare population differences in latrine-based communication networks along a rural-to-urban gradient. The paucity of studies investigating the relative importance of core marking (*within-group communication*) vs. peripheral marking (*between-group communication*) in mammalian latrine-based communication networks further motivated our present study. We investigated rabbit populations along a rural-to-urban gradient. We located latrines at each site and established the distance of each latrine to the nearest burrow. We also assessed latrine dimensions and densities as indicators for long-term use, and numbers of fresh fecal pellets as an indicator for recent use. We further quantified direct and indirect anthropogenic impact at our study sites, including several (interrelated) variables describing human nuisance and anthropogenic landscape alterations (see 'degree of urbanity' [23, 31]). This allowed us to establish distribution patterns of latrines relative to the burrow, whereby a prevalence of *core marking* should be reflected by highest latrine densities, larger latrine dimensions, and more fecal pellets per latrine, close to the burrow compared to latrines afar from it. If *peripheral marking* prevails, this should lead to the opposite pattern.

Our predictions were derived from the observation that population densities of rabbits increase, while at the same time social group sizes decrease, along the rural-to-urban gradient considered here [23, 31]. We predicted that *peripheral marking* for territorial defense becomes more important in urbanized regions, as increasing population densities increase competition for space and other resources. Moreover, small group sizes at urban study sites should also favor peripheral over core marking behavior as the necessity to communicate within groups decreases. This should lead to a pattern where latrine densities, sizes, and utilization frequencies increase with increasing distance from the burrow towards the inner parts of the city, while the opposite pattern can be predicted for rural sites.

Methods

Selection of study sites

We studied rabbit populations in nine green spaces (measuring between 1 and 4.9 ha in size) in the city center of Frankfurt a.M. (Germany) that are highly fragmented and separated from each other by heavily used roads, in four parks at the periphery of the city (between 5.5 and 30.2 ha) and at two nearby rural study sites (both 36 ha; Table 1; Figs. 1, 2). Unfortunately, we were not able to include more study sites within the rural surrounding of Frankfurt a.M. due to difficulties in finding areas where a representative population density is still existent.

Table 1 Study sites

Study sites	Coordinates		Size [ha]	Degree of urbanity	Population density (rabbits/ha)	Mean social group size
Rural						
Bad Vilbel	N 50°9.418	E 8°41.820	36.00	−2.55	0.88	8.80
Maintal	N 50°8.653	E 8°49.094	36.00	−1.80	3.38	10.00
Suburban						
Ostpark	N 50°7.251	E 8°43.364	30.20	−0.45	19.14	9.50
Grüneburgpark	N 50°7.647	E 8°39.608	27.00	−0.43	0.26	3.50
Rebstockpark	N 50°6.674	E 8°36.773	21.10	−0.36	15.02	4.00
Miquelanlage	N 50°7.970	E 8°39.524	5.50	−0.04	2.27	2.83
Urban						
Site 1	N 50°6.999	E 8°41.503	4.90	0.47	8.16	2.90
Site 2	N 50°6.673	E 8°41.608	3.53	0.47	4.53	4.00
Site 3	N 50°6.723	E 8°40.220	3.64	0.50	9.07	4.00
Site 4	N 50°7.098	E 8°40.946	3.37	0.57	13.95	2.00
Site 5	N 50°7.160	E 8°41.198	2.18	0.59	15.60	3.40
Site 6	N 50°7.001	E 8°40.529	3.66	0.59	3.55	2.00
Site 7	N 50°6.865	E 8°40.263	1.33	0.76	9.02	1.50
Site 8	N 50°6.870	E 8°41.650	1.50	0.84	24.67	1.67
Site 9	N 50°6.606	E 8°40.323	1.00	0.85	5.00	2.00

Detail information for the 15 study sites situated along the rural-to-urban gradient in and around Frankfurt a.M., Germany

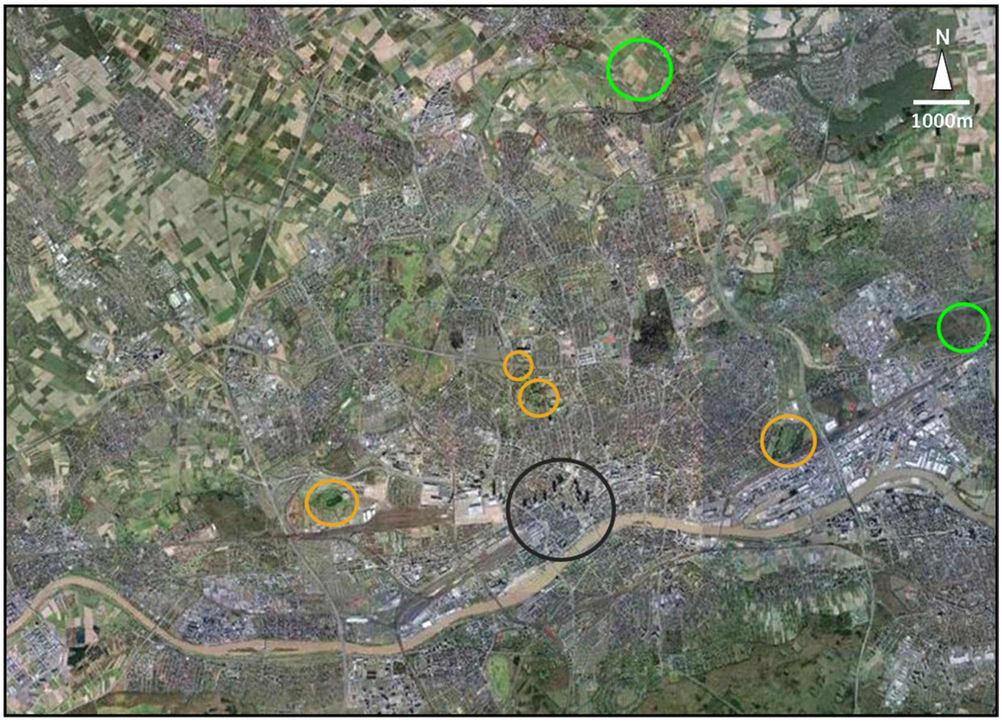

Fig. 1 Overview and location of study sites. Locations of all 15 study sites along the rural-to-urban gradient in and around Frankfurt a.M. *Black circles* $n = 9$ urban study sites, *orange circles* $n = 4$ suburban study sites, *green circles* $n = 2$ rural study sites *Source* Google Earth

In case of the suburban and urban study sites, short-cut meadows were the dominant landscape element (with a grass cutting regime of up to once a week during summer), and the dimensions of our study sites were clearly defined by park borders like streets or pathways. As comparable structures were lacking at both rural sites, we decided to selected quadrants of 600 × 600 m as our study sites, which were sufficiently large to include the outermost latrines afar from the burrow systems (Fig. 2). Here, open landscapes were dominated by agriculturally used areas where meadows (with a sheep grazing regime of two times per year), rape and wheat fields alternated. Between the meadows and fields, only few patches of thickets were present, mainly comprising blackberry bushes (Fig. 2).

Survey of latrine-based communication networks

We systematically mapped latrines and burrows by two persons walking line transects (app. 5 m apart) across the entire study area within all of our 15 study sites, starting in the early morning. We took GPS coordinates from the center of 3253 latrines and the center of 182 burrow systems using a Garmin 12 GPS [separate burrow systems were identified with the help of local hunters that use domesticated ferrets (*Mustelo putorius furo*) to chase rabbits out of the burrow within the framework of a regular hunting scheme, organized by the city of Frankfurt, hunting licence ID 1000250221]. We collected data during the reproductive season of rabbits, which in our latitude lasts from March to September, when territorial defense is strongest [36, 38]. Urban and suburban study sites as well as the rural study site Bad Vilbel were simultaneously sampled between May and September 2011, while the second rural study site (Maintal) was sampled between June and July 2012. Latrines were defined as an accumulation of at least 20 single fecal pellets within an area of 20 × 30 cm [44]. Based on the GPS coordinates we calculated distances of latrines to the nearest burrow system (see also [33, 35, 45]). We measured several variables for each latrine that are—according to previous studies on mammals, including European rabbits—suitable to characterize latrine-based communication networks [4, 6, 9, 11, 12, 33, 36]. Later we evaluated how those variables change with increasing distance of latrines from the respective burrow system (core vs. peripheral marking, see Statistical analyses). For example, if core marking prevails, latrines close to the burrow should be used more often by the members of the social group than peripheral ones, and this should be reflected by higher numbers of (fresh) fecal pellets compared to latrines that are less often used.

Fig. 2 Example of latrine distribution patterns. Detailed aerial photograph of the study site Bad Vilbel. *White triangles* indicate rabbit burrows, *white dots* indicate rabbit latrines *Source* Google Earth

We excluded $n = 10$ burrow systems with less than three latrines from our statistical analyses as those burrows did not show signs of regular use. Moreover, by doing so, we followed the methodological approach of another recent study on latrine distribution patterns of European rabbits in a suburban area [33] so that we were able to discuss our results in comparison to that study.

(a) Indicators of long-term latrine use

As one indicator of long-term latrine use, we established latrine sizes by measuring the maximum width and length of the area that fell into our definition of a latrine (see above). We approximated latrine dimensions [m^2] using a rectangular formula. We also determined numbers of fecal pellets per latrine as another estimate of latrine size. Accurately counting fecal pellets in all latrines through total clearing would have caused an enormous work load, and so we decided to estimate numbers of fecal pellets by eye (see [36]). This estimation method had been practiced before data collection at sites outside of our study area and was confirmed through total clearing after the test trials. As latrine sizes and numbers of fecal pellets both describe latrine dimensions, we log-transformed and subjected both to a factor reduction (principal component analysis, PCA). We retrieved a single PC with an Eigenvalue >1 (1.50) that explained 75.3 % of the total variance, henceforth referred to as 'latrine dimension'.

Another variable that was used in previous studies to describe the relative importance of core vs. peripheral marking was the latrine density (e.g., latrines were more densely packed at the territorial periphery in a high-density urban badger population [16]). We expressed latrine densities by calculating the mean distance of each latrine to the nearest two neighboring latrines [11, 12].

(b) Indicator of recent latrine use

As an indicator of recent latrine use, we noted whether fresh fecal pellets were present ('0' no fresh fecal pellets present, '1' fresh fecal pellets present) and if present, we accurately counted them once during the process of latrine mapping in the early morning (see [36]).

(c) Indicator of territorial behavior at latrines

We noted whether rabbit paw-scrapings—signs of male territorial behavior [46, 47]—were present at latrines ('0' no paw-scrapings present, '1' paw-scrapings present).

However, we were unable to accurately quantify actual numbers of paw-scrapings.

(d) Effect of woody vegetation on latrine distribution

Finally, we also determined the distance of each latrine to the next woody vegetation (either shrubs or a tree), as this ecological variable is known to affect the placement and utilization frequency of latrines in European rabbits [33, 35].

Estimating the impact of urbanization

In order to relate (direct and indirect) anthropogenic influences to potential differences in latrine-based communication networks we calculated the 'degree of urbanity' for each of our 15 study sites following previous studies [23, 31]. In brief, we assessed the proportion of artificial ground cover (e.g., streets, play grounds) and numbers of anthropogenic objects per ha (e.g., benches, street lamps) at each study site, reflecting the availability of continuous living space. Information on the direct intensity of disturbance by humans (pedestrians and bikers) and leashed or unleashed dogs (per min and per ha) that rabbits were exposed to during their main activity periods at dusk and dawn was obtained through transect counts (for more details see [23, 31]). Additionally, we obtained data on numbers of human residents located within a radius of 500 m from the borders of the study sites from the registration office of Frankfurt a.M. (*Einwohnermeldeamt*, updated: 31.10.2010). These data provide an estimation of overall/peak numbers of visitors in the park areas, as residents tend to walk in nearby city parks.

We subjected the four (log-transformed) variables to PCA. A single principal component was retrieved (henceforth referred to as the PC 'degree of urbanity', Table 1) with an Eigenvalue >1 (3.44) that explained 85.9 % of the total variance (Table 2a). For display purpose only, study sites were categorized as rural ('degree of urbanity' values ≤ -0.5), suburban (> -0.5 and ≤ 0.5) and urban (>0.5), while the main statistical analyses were performed using continuous data (see below).

To establish a variable characterizing rabbit population dynamics, we relied on previously published data on rabbit densities (numbers of individuals per ha, assessed by direct census counts along pre-defined transects during dusk and dawn in September/October 2011; Table 1; [31]) and burrow densities [23, 31]. Moreover, we included data on social group sizes, obtained through behavioral observations and augmented by the use of ferrets to drive all members of a social group out of their burrow (Table 1; [23]). Again, we log-transformed the three variables and subjected them to PCA. A single principal component was retrieved with an Eigenvalue >1 (2.00) that explained 66.7 % of the total variance (PC 'population dynamics'; Table 2b). As both principal components, the 'degree of urbanity' and 'population dynamics', were highly correlated (Spearman rank correlation: $r = 0.74$, $p = 0.002$, $n = 15$; see also [23, 31]), we decided to include only the 'degree of urbanity' in our statistical analyses. Running independent analytical models (see below) with different combinations of both covariates (e.g., 'population dynamics' and 'degree of urbanity'), however, yielded qualitatively very similar results (results not shown).

Table 2 Degree of urbanity and rabbit population dynamics

	Axis loading
(*a*) Urbanization-related variables	
Proportion of artificial ground cover at each study site	0.84
Numbers of anthropogenic objects per ha at each study site	0.93
Intensity of disturbance by humans and leashed/unleashed dogs min^{-1} ha^{-1}	0.97
Numbers of human residents located within a radius of 500 m	0.96
(*b*) Variables related to population dynamics	
Population density	0.89
Burrow density	0.94
Social group size	−0.58

Axis loadings of two separated principal component analyses on variables related to (*a*) urbanization effects (explaining 85.9 % of the total variance) and (*b*) rabbit population dynamics, respectively (explaining 66.7 % of the total variance)

Statistical analyses

(a) Relative distance of latrines to the nearest burrow (d_{rel})

To compare the spatial distribution of latrines between sites, we first corrected for variation in the sizes of areas marked by latrines around burrow systems, e.g., different home range sizes. Unfortunately, radio-tracking and capture-mark-recapture approaches to establish exact home range dimensions were not feasible for all rabbit groups at our 15 study sites. By using the following approach we were still able to account for variation in home range sizes:

First, based on a distance matrix for all latrines and all burrows at a given study site, each latrine was assigned to the closest burrow (see also [33, 35]). Second, for each burrow we defined the perimeter in which 95 % of all latrines that had been assigned to this burrow were located. Third, we determined the mean distance of the two outermost latrines to the rabbit burrow within this 95 % perimeter (d_{max}) and used this value to calculate the dimensions of the latrine-marked area (A [ha]) around each rabbit burrow, assuming the burrow to be the center ($A = \pi \times d_{max}^2$). For every latrine belonging to this burrow system we corrected its absolute distance to the center of the burrow (d_{abs}) by d_{max} and thus obtained the relative distance of a latrine as $d_{rel} = d_{abs}/d_{max}$. Our approach was justified by the observation that we found latrines that were located close to the respective burrow system and afar from it in all cases, representing cases of core- and peripheral marking (see also [33]). Where we provide descriptive statistics, we categorized latrines depending on d_{rel}-values as ≤0.25 (e.g., around the burrow), 0.25–0.50, 0.50–0.75, or ≥0.75 (periphery), while all statistical tests were conducted using continuous data.

In our first approach, we used arcsine (square root)-transformed d_{rel}-values as the dependent variable in a linear mixed model (LMM, 'mixed' procedure in SPSS 13). We used 'burrow ID' as subject-grouping factor with random intercepts specified for each burrow and the 'degree of urbanity' as the explaining variable (covariate). A similar approach was used to investigate a potential effect of increasing urbanity on latrine-marked areas around rabbit burrows.

(b) Latrine characteristics in relation to the distance to the nearest burrow

In our second approach, we tested whether latrine dimensions and densities, numbers of fresh fecal pellets and distances to the next woody vegetation differed from the core to the periphery of the latrine-marked area, and if this pattern changes along the rural-to-urban gradient. We ran four LMMs using the respective variables (all log-transformed) and again included random intercepts for every burrow system ('burrow ID'), while 'd_{rel}'-values and the 'degree of urbanity' were used as explaining variables (covariates).

We included the interaction term 'd_{rel} × degree of urbanization' in the initial model and step-wise removed all non-significant explaining variables from the reduced model starting with the interaction effect. In case of significant interaction terms, we refrained from interpreting main effects and concentrated on the interaction effects. To analyze the binary variables 'presence of fresh fecal pellets' and 'presence of paw-scrapings' we ran logistic regressions each including 'd_{rel}', the 'degree of urbanity', and their interaction as the explaining variables. Non-significant effects were excluded in a step-wise backwards elimination procedure.

Results

Relative distance of latrines to the nearest burrow (d_{rel})

The 'degree of urbanity' had a significant effect on mean distances of latrines to the next burrow system (d_{rel}; Table 3a), reflecting that distribution patterns of latrines shifted from core- to more periphery-biased along the rural-to-urban gradient. At rural sites, 13.5 ± 0.6 % of all latrines (mean proportion ± SE) were located in the core section close to the burrow ($d_{rel} \leq 0.25$) and 25.3 ± 1.6 % at the relative periphery ($d_{rel} \geq 0.75$). By contrast, only 3.4 ± 1.1 % of latrines were established within the core section at urban study sites, while 34.6 ± 7.0 % of latrines was found at the periphery of the latrine-marked area. At suburban study sites, 11.7 ± 2.1 % of latrines were located in the core section and 33.2 ± 4.7 % at the periphery.

We also detected a significant effect of the 'degree of urbanity' on the dimensions of the latrine-marked area around rabbit burrows ('Latrine-marked area'; Table 3b), which decreased from 2.73 ± 0.48 ha at rural sites, over 2.11 ± 0.27 ha at suburban sites, to 0.87 ± 0.25 ha at urban study sites.

Latrine characteristics in relation to their distance to the nearest burrow

(a) Indicators of long-term latrine use

Latrine dimensions were affected by the 'degree of urbanity' and the interaction term 'd_{rel} × degree of urbanity' ('Latrine dimension'; Table 3c). While latrine dimensions at rural study sites became smaller with increasing distance from the next burrow (Fig. 3a), the opposite pattern was observed at urban study sites: latrines that were located at the relative periphery of the latrine-marked area were larger than those located close to the burrow (Fig. 3c). Regarding suburban sites, latrine sizes showed

Table 3 Univariate linear mixed models

Fixed effects	*F*	*df*$_1$, *df*$_2$	*P*
(*a*) d_{rel}			
'Degree of urbanity'	11.13	1, 93	0.001
(*b*) Latrine-marked area (A)			
'Degree of urbanity'	25.49	1, 126	<0.001
(*c*) Latrine dimension (PC on latrine size and numbers of fecal pellets)			
'Degree of urbanity'	3.04	1, 531	<0.001
'd_{rel}'	0.29	1, 2960	0.589
'd_{rel} x degree of urbanity'	5.33	1, 2870	<0.001
(*d*) Latrine density			
'Degree of urbanity'	10.67	1, 190	0.001
'd_{rel}'	34.74	1, 2953	<0.001
'd_{rel} x degree of urbanity'	5.26	1, 2900	0.022
(*e*) Numbers of fresh fecal pellets			
'Degree of urbanity'	0.77	1, 269	0.38
'd_{rel}'	0.91	1, 295	0.34
'd_{rel} x degree of urbanity'	0.98	1, 521	0.32
(*f*) Distance to next woody vegetation			
'Degree of urbanity'	11.31	1, 2973	0.001
'd_{rel}'	354.29	1, 2853	<0.001

Results of univariate LMMs using (*a*) 'd_{rel}', (*b*) 'latrine-marked area (A)', (*c*) 'latrine dimension', (*d*) 'latrine density', (*e*) 'numbers of fresh fecal pellets' and (*f*) 'distance to next woody vegetation' as dependent variables

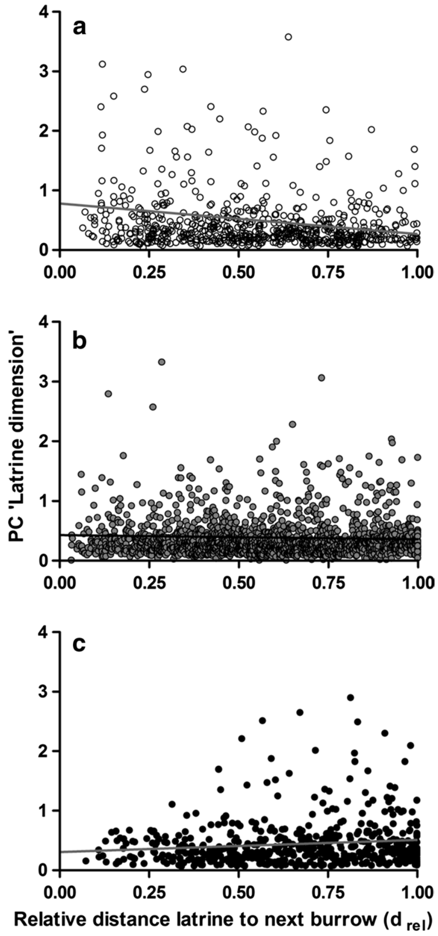

Fig. 3 Latrine dimension. Correlation between the PC 'latrine dimension' (incorporating the size of latrines [m^2] and numbers of fecal pellets) and the relative distance to the next burrow (d_{rel}) at (**a**) rural sites with 'degree of urbanity' values ≤ -0.5 ($n = 547$ latrines), (**b**) suburban sites with 'degree of urbanity' values > -0.5 and ≤ 0.5 ($n = 1828$), and (**c**) urban sites with 'degree of urbanity' values >0.5 ($n = 652$ latrines)

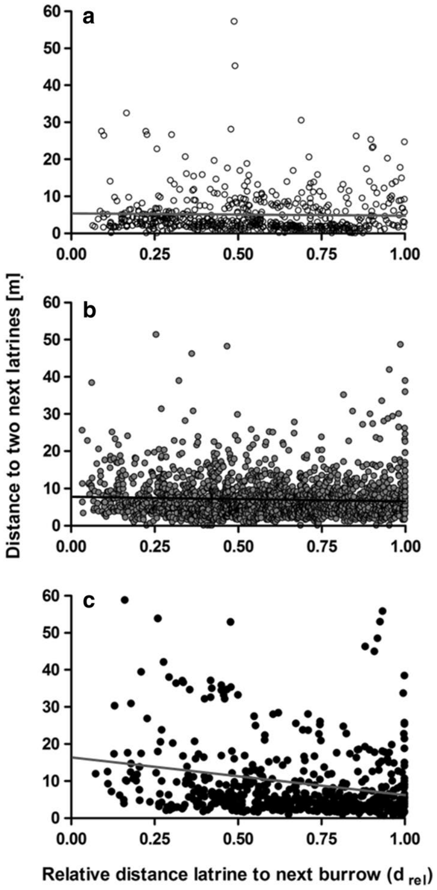

Fig. 4 Latrine density. Correlation between latrine density (expressed by the mean distance of a latrine to the nearest two neighboring latrines [m]) and the relative distance to the next burrow (d_{rel}) at (**a**) rural sites with 'degree of urbanity' values ≤ -0.5 ($n = 547$ latrines), (**b**) suburban sites with 'degree of urbanity' values > -0.5 and ≤ 0.5 ($n = 1828$), and (**c**) urban sites with 'degree of urbanity' values >0.5 ($n = 652$ latrines)

no notable variation within the latrine-marked area (Fig. 3b).

Considering latrine densities, the 'degree of urbanity', 'd_{rel}' and the interaction term 'd_{rel} × degree of urbanity' had significant effects ('Latrine density'; Table 3d). The latrine density decreased slightly with increasing distance from the next burrow system at rural study sites (Fig. 4a). By contrast, at urban sites latrine densities were considerably higher at the relative periphery of the latrine-marked area compared to latrines located close to the burrow (Fig. 4c). At suburban study sites, latrine densities did not vary throughout the latrine-marked area (Fig. 4b).

(b) Indicator of recent latrine use

As an estimate of the frequency of recent latrine use, we analyzed presence of fresh fecal pellets in each latrine. The logistic regression revealed a negative correlation between the 'degree of urbanity' and the presence of fresh fecal pellets within latrines ($B = -0.17$, $Wald = 13.96$, $SE = 0.046$, $P < 0.001$, $-2\log$ likelihood $= 2884.71$, Nagelkerke $R^2 = 0.007$; all excluded variables: $P \geq 0.29$), suggesting that the proportion of latrines that contain fresh fecal pellets decreased along the rural-to-urban gradient. Considering only the subset of latrines that contained fresh fecal pellets, our mixed model revealed no significant relations between the dependent and independent variables ('Numbers of fresh fecal pellets'; Table 3e).

(c) Indicator of territorial behavior at latrines

Regarding the presence of paw-scrapings at latrines the logistic regression uncovered a positive correlation with the 'degree of urbanity': the proportion of latrines at which paw-scrapings were present increased along the rural-to-urban gradient ($B = 0.57$, $Wald = 176.27$, $SE = 0.043$, $P < 0.001$, $-2\log$ likelihood $= 3637.78$, Nagelkerke $R^2 = 0.083$; all excluded variables: $P \geq 0.38$). In 76.6 ± 2.0 % of all latrines mapped at urban study sites paw-scrapings were present (mean percent latrines with paw-scrapings present ± SE), while this was only the case in 43.8 ± 1.8 % of all latrines at rural study sites and 70.4 ± 1.1 % of latrines at suburban sites.

(d) Effect of woody vegetation on latrine distributions

Finally, the distance of latrines to the next woody vegetation was affected by 'd_{rel}' and the 'degree of urbanity' ('Distance to next woody vegetation'; Table 3f). The distance between latrines and the next tree or shrub increased with increasing distance from the burrow, reflecting that most burrows were situated in dense vegetation. At core sections ($d_{rel} \leq 0.25$), the mean (± SE) distance of latrines to the next woody vegetation was 8.72 ± 0.98 m ($n = 318$), while at the periphery ($d_{rel} \geq 0.75$) mean distances were 16.10 ± 0.58 m ($n = 896$). Along the rural-to-urban gradient, the mean distance of latrines to the next woody vegetation was shortest for urban areas (5.66 ± 0.69 m, $n = 652$) compared to rural (14.95 ± 0.65 m, $n = 547$) and suburban sites (16.83 ± 0.38 m, $n = 1828$).

Discussion

Our present study is the first to demonstrate gradual variation in the relative importance of different latrine marking strategies in European rabbit populations along a rural-to-urban gradient. The results comply with our prediction that higher rabbit population densities in urban regions, along with smaller group sizes (pairs and their offspring, and partly even solitary individuals [23, 31]), bring about an increased necessity for *between-group communication*, e.g., to claim territorial occupancy through peripheral marking. Not only were relatively more latrines located at the periphery of the rabbit burrow in urban populations, but those latrines were also larger in size, more densely packed and more frequently used. This trend contrasted with a strong signature of core marking in rural rabbit populations.

Fewer group members contributing to the establishment and maintenance of latrine-based communication networks in urban rabbit populations likely explain why the proportion of latrines with fresh fecal pellets was lower. Moreover, higher ambient temperatures and altered patterns of precipitation and evaporation are typical of urban regions—caused by the high proportion of sealed surfaces [48, 49]—possibly accelerating the decay of fecal pellets. Also, some fecal pellets will be regularly removed during the maintenance of green spaces, which, according to information provided by the *Frankfurter Grünflächenamt*, reaches its maximum in urban parks. Accordingly, using numbers of fecal pellets and fresh fecal pellets, respectively, as dependent variables to characterize latrine-based communication networks in urban, suburban and rural mammalian populations needs to be considered with caution. Likewise, those variables are sometimes used to estimate local rabbit population densities, which can also provide misleading information (see also [50]). Competition for space and other resources in the small and highly fragmented urban parks is probably intense, given that both the proportion of sealed surface areas and population densities were high, while home range areas marked by latrines were small. We argue that strong competition brings about an increased importance of peripheral marking behavior (see also [15–17]). This is also reflected by the fact that more paw-scrapings (which males use for territory demarcation) were found in latrines at urban study sites.

Following Domínguez-Cebrían and de Miguel [33], another important factor that likely affects latrine-based communication networks in rabbits is predation risk [33, 51]. Common predators of European rabbits in Germany can also reach high densities in cities (foxes [20]; mustelids like *Martes foina* and *Mustela erminea* [30]; domestic cats [52]; crows, *Corvus corone* and magpies, *Pica pica* that prey on juvenile rabbits [53]). However, the fact that those species can reach high densities in cities does not necessarily mean that they exert strong predation on urban rabbit populations ("the predation paradox" [54], reviewed in [22]). For example, several studies demonstrated that those predators can use other abundant food sources in cities [22, 55]. Moreover, both, predator and prey species can alter their activity patterns in urban regions, again leading to an altered predator exposure [56]. Unfortunately, we were not able to systematically quantify predation risk at our study sites. Still, decreased flight initiation distances in suburban and urban rabbits [31] and less time spent exhibiting anti-predator behavior [32] suggest that predation of urban and suburban rabbits may indeed be lower compared to rural populations. At rural sites, rabbits that use latrines at the periphery of their home ranges may be more exposed to predators, while reduced predation risk in urban populations leaves more time to establish and maintain complex communication networks involving latrines afar from the burrow.

When considering distances between latrines and the nearest woody vegetation, shorter distances in urban areas likely reflect more heterogeneous landscapes in cities [54, 56]. In contrast, rural study sites were mostly agriculturally used and are characterized by open and homogeneous landscapes with scarce woody vegetation. In line with the interpretation that sufficient shelter (shrubs and trees) eases burrow formation, a previous study found burrows to become more uniformly distributed along the rural-to-urban gradient considered here [23]. Rabbits prefer to establish latrines on bare soil, clearings, or elevated areas, often close to conspicuous landscape elements such as bushes, trees or anthropogenic objects, while avoiding densely vegetated areas [33, 36]. Not only does this increase the visibility and accessibility of latrines, but it could also reduce the risk of falling victim to avian and terrestrial predators during latrine visits [35]. At our rural study sites, most latrines were found on meadows with short grass, especially close to pathways, while crop fields were largely avoided. By contrast, landscape elements appear to not have such a strong effect on latrine distribution patterns at suburban and urban study sites, where meadows with short grass prevailed.

In contrast to European rabbits, groups of European badgers showed no peripheral marking behavior in urban regions—even at the few sites where the home ranges of different groups overlapped [25, 26]. Davison et al. [26] argued that urban badger groups were rather isolated even where population densities were high, reducing the need for territory demarcation (see also [25]). This was clearly not the case in our study, in which distinct social groups of rabbits occupied territories in close proximity to one another at urban and suburban study sites. Furthermore, crepuscular, timid species like badger are less likely to habituate to permanent anthropogenic disturbance compared to European rabbits (see above). Badgers are probably more distracted from latrine marking by human disturbance than rabbits (see also [4]). Moreover, badger home ranges are considerably larger than those of European rabbits (mean 95 % kernel group home range sizes of urban badgers: 4.71 [26] vs. 0.62 ha for suburban and urban European rabbit populations, unpubl. data). This renders peripheral marking in badgers even more challenging under intense anthropogenic disturbance.

Conclusions

Human activities affect urban wildlife populations, e.g., through anthropogenic nuisance, habitat fragmentation, and altered food availability (reviewed in [22, 29]). Behavioral changes in urban populations compared to populations inhabiting rural areas (like altered flight- or ranging behavior [22, 29]) are often interpreted as a *direct* consequence of animals having to cope with those novel ecological conditions. Our present study demonstrates behavioral changes in European rabbits, namely altered distribution patterns of latrines relative to the corresponding burrow. Based on previous studies on this and other mammalian species, we argue that increased peripheral marking in urban populations reflects an increased importance of *between-group communication* (rather than *within-group communication*), and this seems to be a consequence of higher population densities, smaller group sizes, and altered predation risk. Our study adds to our knowledge about the function of mammalian latrines as centers for information exchange between individuals, and—more generally—points towards *indirect* effects of anthropogenic landscape alteration and human nuisance on the behavior of urban wildlife populations. If our interpretations are correct, our results have implications for the conservation and management of rabbit populations: while rural rabbit populations suffer from a loss of suitable habitat [23, 31, 41–44], rabbit populations in urban areas might show higher intrinsic mortality rates arising from high intraspecific competition, while suburban habitats may currently provide an advantageous combination of structural heterogeneity and comparatively low levels of competition. Ongoing studies are trying to assess the potential role of cities in the future conservation of this species, e.g., by providing population genetic information on potential source-sink dynamics in population development. Another aspect to be considered in future studies is that urban and suburban rabbit populations may serve as ecosystem engineers; e.g., nutrients accumulate at latrines, which could have implications for local plant communities and possibly seed dispersal [56, 57]. As "fertile islands", latrines likely further increase habitat heterogeneity in urban and suburban landscapes [57].

Abbreviations

a.M.: am Main; d_{max}: maximum distance of a latrine to the center of the next burrow; d_{rel}: relative distance of a latrine to the center of the next burrow; d_{abs}: absolute distance of a latrine to the center of the next burrow.

Authors' contributions

Conceived and designed the experiments: MZ, SM, TW and MP. Collected data: MZ, SB, A-LB, MB, SW. Analyzed the data: MZ, DB, BG. Contributed analysis tools: BG. Wrote the paper: MZ, TW and MP. All authors read and approved the final manuscript.

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Availability of data and materials
In addition to the data available in the manuscript itself further datasets supporting the conclusions of this article are available [58].

Competing interests
The authors declare that they have no competing interests.

Ethics approval and consent to participate
Our study on the behavioral ecology of European rabbits complies 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). No animals were killed or manipulated, i.e., data collection was non-invasive. A consent to participate is not applicable.

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References

1. MacDonald DW. Patterns of scent marking with urine and faeces amongst carnivore communities. Symp Zool Soc Lond. 1980;45:107–39.
2. Gorman ML, Trowbridge BJ. The role of odor in the social lives of carnivores. In: Gittleman JL, editor. Carnivore behavior, ecology, and evolution. Berlin: Springer; 1989. p. 57–88.
3. Gorman ML. Scent marking strategies in mammals. Rev Suisse Zool. 1990;97:3–29.
4. Dröscher I, Kappeler PM. Maintenance of familiarity and social bonding via communal latrine use in a solitary primate (*Lepilemur leucopus*). Behav Ecol Sociobiol. 2014;68:2043–58.
5. Roper TJ, Shepherdson DJ, Davies JM. Scent marking with faeces and anal secretion in the European badger (*Meles meles*): seasonal and spatial characteristics of latrine use in relation to territoriality. Behaviour. 1986;97:94–117.
6. Roper TJ, Conradt L, Butler J, Christian SE, Ostler J, Schmid TK. Territorial marking with faeces in badgers (*Meles meles*): a comparison of boundary and hinterland latrine use. Behaviour. 1993;127:289–307.
7. Irwin MT, Samonds KE, Raharison JL, Wright PC. Lemur latrines: observations of latrine behavior in wild primates and possible ecological significance. J Mammal. 2004;85:420–7.
8. Jordan NR, Cherry MI, Manser MB. Latrine distribution and patterns of use by wild meerkats: implications for territory and mate defence. Anim Behav. 2007;73:613–22.
9. Wronski T, Apio A, Plath M. The communicatory significance of localised defecation sites in bushbuck (*Tragelaphus scriptus*). Behav Ecol Sociobiol. 2006;60:368–78.
10. Kruuk H. Spatial organization and territorial behavior of the European badger *Meles meles*. J Zool. 1978;184:1–19.
11. Wronski T, Plath M. Characterization of the spatial distribution of latrines in reintroduced mountain gazelles (*Gazella gazella*): do latrines demarcate female group home ranges? J Zool. 2010;280:92–101.
12. Wronski T, Apio A, Plath M, Ziege M. Sex difference in the communicatory significance of localized defecation sites in Arabian gazelles (*Gazella arabica*). J Ethol. 2013;31:129–40.
13. Mykytowycz R, Gambale S. The distribution of dung-hills and the behavior of free living wild rabbits, *Oryctolagus cuniculus* (L.), on them. Forma Funct. 1969;1:333–49.
14. Mykytowycz R, Hesterman ER, Gambale S, Dudzińsky ML. A comparison of the effectiveness of the odors of rabbits, *Oryctolagus cuniculus*, in enhancing territorial confidence. J Chem Ecol. 1976;2:13–24.
15. Schley L, Schaul M, Roper TJ. Distribution and population density of badgers *Meles meles* in Luxembourg. Mamm Rev. 2004;34:233–40.
16. Hutchings MR, Service KM, Harris S. Is population density correlated with faecal and urine scent marking in European badgers (*Meles meles*) in the UK? Mamm Biol. 2002;67:286–93.
17. Myers K, Poole WE. A study of the biology of the wild rabbit, *Oryctolagus cuniculus* (L.), in confined populations. I. The effects of density on home range and the formation of breeding groups. CSIRO Wildl Res. 1959;4:14–26.
18. Gosling LM, Roberts SC. Testing ideas about the function of scent marks in territories from spatial patterns. Anim Behav. 2001;62:F7–10.
19. Francis RA, Chadwick MA. What makes a species synurbic? Appl Geogr. 2012;32:514–21.
20. Gloor S, Bontadina F, Hegglin D, Deplazes P, Breitenmoser U. The rise of urban fox populations in Switzerland. Mamm Biol. 2001;66:155–64.
21. Prange S, Gehrt SD, Wiggers EP. Demographic factors contributing to high raccoon densities in urban landscapes. J Wildl Manag. 2003;67:324–33.
22. Rodewald AD, Gehrt SD. Wildlife Population Dynamics in Urban Landscapes. In: McCleery RA, Moorman CE, Peterson MN, editors. Urban wildlife conservation—theory and praxis. Berlin: Springer; 2014. p. 117–47.
23. Ziege M, Brix M, Schulze M, Seidemann A, Straskraba S, Wenninger S, Streit B, Wronski T, Plath M. From multifamily residences to studio apartments—shifts in burrow structures of European rabbits along a rural-to-urban gradient. J Zool. 2015;295:286–93.
24. Harris S. Activity patterns and habitat utilization of badgers (*Meles meles*) in suburban Bristol: a radio tracking study. In: symposia of the zoological society of London. Vol. 49. Published for the Zoological Society by Academic Press; 1982. p. 301–23.
25. Cresswell WJ, Harris S. Foraging behavior and home-range utilization in a suburban badger (*Meles meles*) population. Mamm Rev. 1988;18:37–49.
26. Davison J, Huck M, Delahay RJ, Roper TJ. Restricted ranging behavior in a high-density population of urban badgers. J Zool. 2009;277:45–53.
27. Bozek CK, Prange S, Gehrt DS. The influence of anthropogenic resources on multi-scale habitat selection by raccoons. Urban Ecosyst. 2007;10:413–25.
28. Adkins CA, Stott P. Home ranges, movements and habitat associations of red foxes *Vulpes vulpes* in suburban Toronto, Ontario, Canada. J Zool. 1998;244:335–46.
29. Ryan AM, Partan SR. Urban wildlife behavior. In: McCleery RA, Moorman CE, Peterson MN, editors. Urban wildlife conservation—theory and praxis. Berlin: Springer; 2014. p. 149–73.
30. Duduś L, Zalewski A, Kozioł O, Jakubiec Z, Król N. Habitat selection by two predators in an urban area: the stone marten and red fox in Wrocław (SW Poland). Mamm Biol. 2014;79:71–6.
31. Ziege M, Babitsch D, Brix M, Kriesten S, Seidemann A, Wenninger S, Plath M. Anpassungsfähigkeit des Europäischen Wildkaninchens entlang eines rural-urbanen Gradienten. Beiträge zur Jagd- und Wildtierforsch. 2013;38:189–99.
32. Ziege M, Babitsch D, Brix M, Kriesten S, Straskraba S, Wenninger S, Wronski, T, Plath M. Extended diurnal activity patterns of European rabbits along a rural–to–urban gradient. Submitted to Mamm Biol—Zeitschrift für Säugetierkd. 2016.
33. Domínguez-Cebrían I, de Miguel FJ. Selected factors influencing the spatial relationship between latrines and burrows in rabbits *Oryctolagus cuniculus* (L.) in a suburban area of Madrid (Spain). Pol J Ecol. 2013;61:819–23.
34. Mykytowycz R. Territorial marking by rabbits. Sci Am. 1968;218:116–26.
35. Monclús R, de Miguel FJ. Distribución espacial de las letrinas de conejo (*Oryctolagus cuniculus*) en el Monte de Valdelatas (Madrid). Galemys. 2003;15:157–65.
36. Sneddon IA. Aspects of olfaction, social behavior and ecology of an island population of the European rabbit (*Oryctolagus cuniculus*). Ph.D. Thesis, Scotland: St. Andrews University; 1984.
37. Sneddon IA. Latrine use by the European rabbit (*Oryctolagus cuniculus*). J Mammal. 1991;72:769–75.
38. Hesterman ER, Mykytowycz R. Some observations on the odours of anal gland secretions from the rabbit, *Oryctolagus cuniculus* (L.). CSIRO Wildl Res. 1968;13:71–81.
39. Mykytowycz R. Territorial function of chin gland secretion in the rabbit, *Oryctolagus cuniculus* (L.). Nature. 1962;193:799.

40. Mykytowycz R, Hesterman ER. The behavior of captive wild rabbits, *Oryctolagus cuniculus* (L.) in response to strange dung-hills. Forma Funct. 1970;2:1–12.
41. Lees AC, Bell DJ. A conservation paradox for the 21st century: the European wild rabbit *Oryctolagus cuniculus*, an invasive alien and an endangered native species. Mamm Rev. 2008;38:304–20.
42. Ferreira C, Touza J, Rouco C, Díaz-Ruiz F, Fernandez-de-Simon J, Ríos-Saldaña CA, Ferreras P, Villafuerte R, Delibes-Mateos M. Habitat management as a generalized tool to boost European rabbit *Oryctolagus cuniculus* populations in the Iberian Peninsula: a cost-effectiveness analysis. Mamm Rev. 2014;44:30–43.
43. Arnold JM, Greiser G, Keuling O, Martin I, Straus E. Status und Entwicklung ausgewählter Wildtierarten in Deutschland. Jahresbericht 2012. Wildtier-Informationssystem der Länder Deutschlands (WILD), Berlin.
44. Virgós E, Cabezas-Díaz S, Malo A, Lozano J, López-Huertas D. Factors shaping European rabbit abundance in continuous and fragmented populations of central Spain. Acta Theriol (Warsz). 2003;48:113–22.
45. Ruiz-Aizpurua L, Planillo A, Carpio AJ, Guerrero-Casado J, Tortosa FS. The use of faecal markers for the delimitation of the European rabbit's social territories (*Oryctolagus cuniculus* L.). Acta Ethol. 2013;16:157–62.
46. Eisermann K. Long-term heart rate responses to social stress in wild European rabbits: predominant effect of rank position. Physiol Behav. 1992;52:33–6.
47. Bell DJ. Aspects of the social behavior of wild and domesticated rabbits (*Oryctolagus cuniculus*). Cardiff: University of Wales; 1977.
48. Pickett STA, Cadenasso ML, Grove JM, Nilon CJ, Pouyat RV, Zipperer WC, Costanza R. Urban ecological systems: linking terrestrial, ecological, physical, and socioeconomic components of metropolitan areas. Annu Rev Ecol Syst. 2001;32:127–57.
49. Knapp S, Kühn I, Schweiger O, Klotz S. Challenging urban species diversity: contrasting phylogenetic patterns across plant functional groups in Germany. Ecol Lett. 2008;11:1054–64.
50. Barrio IC, Acevedo P, Tortosa FS. Assessment of methods for estimating wild rabbit population abundance in agricultural landscapes. Eur J Wildl Res. 2010;56:335–40.
51. Villafuerte R, Moreno S. Predation risk, cover type, and group size in European rabbits in Doñana (SW Spain). Acta Theriol (Warsz). 1997;42:225–30.
52. Baker PJ, Molony SE, Stone E, Cuthill IC, Harris S. Cats about town: is predation by free-ranging pet cats *Felis catus* likely to affect urban bird populations? Ibis (Lond 1859). 2008;150:86–99.
53. von Holst D, Hutzelmeyer H, Kaetzke P, Khaschei M, Rödel HG, Schrutka H. Social rank, fecundity and lifetime reproductive success in wild European rabbits (*Oryctolagus cuniculus*). Behav Ecol Sociobiol. 2002;51:245–54.
54. Shochat E, Warren PS, Faeth SH, McIntyre NE, Hope D. From patterns to emerging processes in mechanistic urban ecology. Trends Ecol Evol. 2006;21:186–91.
55. Contesse P, Hegglin D, Gloor S, Bontadina F, Deplazes P. The diet of urban foxes (*Vulpes vulpes*) and the availability of anthropogenic food in the city of Zurich, Switzerland. Mamm Biol. 2004;69:81–95.
56. Delibes-Mateos M, Delibes M, Ferreras P, Villafuerte R. Key role of European rabbits in the conservation of the Western Mediterranean Basin Hotspot. Conserv Biol. 2008;22:1106–17.
57. Willott SJ, Miller AJ, Incoll LD, Compton SG. The contribution of rabbits (*Oryctolagus cuniculus* L.) to soil fertility in semi-arid Spain. Biol Fert Soils. 2000;31:379–84.
58. Ziege M, Bierbach D, Bischoff S, Brandt AL, Brix M, Greshake B, Merker S, Wenninger S, Wronski T, Plath M. Field data from latrine mapping of rabbit populations located within urban, suburban and rural study sites in and around Frankfurt am Main. BMC Ecol. 2016. http://www.dx.doi.org/.10.5061/dryad.8s3p0.

Eidesstattliche Erklärung

Ich erkläre hiermit an Eides Statt, dass ich mich bisher keiner Doktorprüfung im Mathematisch-Naturwissenschaftlichen Bereich unterzogen habe und dass ich die vorgelegte Dissertation über

“Effects of gradual anthropogenic habitat alteration on the ecology and behavior of European rabbits (*Oryctolagus cuniculus*) in and around Frankfurt am Main.“

selbstständig angefertigt und mich anderer Hilfsmittel als der in ihr angegebenen nicht bedient habe, insbesondere, dass alle Entlehnungen aus anderen Schriften mit Angabe der betreffenden Schrift gekennzeichnet sind.

Ich versichere, die Grundsätze der guten wissenschaftlichen Praxis beachtet, und nicht die Hilfe einer kommerziellen Promotionsvermittlung in Anspruch genommen zu haben.

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