

Population Genetics, Habitat Use and Nutrition of Wild Boar in Urban Environments

Inaugural-Dissertation
to obtain the academic degree
Doctor rerum naturalium (Dr. rer. nat.)

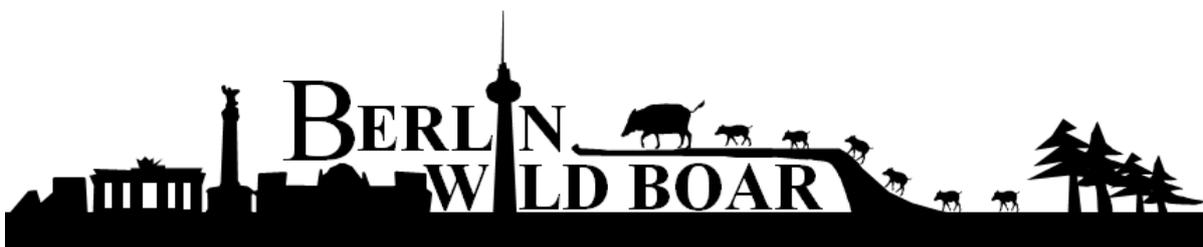
submitted to the Department of Biology, Chemistry and Pharmacy
of Freie Universität Berlin

by

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from Mönchengladbach

2016



The work was conducted at the Leibniz Institute for Zoo and Wildlife Research, beginning in May 2012, until October 2016, supervised by Dr. Stephanie Kramer-Schadt, Dr. Sylvia Ortmann and Prof. Dr. Heribert Hofer.

1. Gutachter: Professor Dr. Heribert Hofer DPhil

2. Gutachter: Prof. Dr. Jörns Fickel

Disputation am 3.4.2017

This thesis is based on the following manuscripts

M. Stillfried¹, J. Fickel^{2,3}, K. Börner¹, U. Wittstatt⁴, M. Heddergott⁵, S. Ortmann¹, S. Kramer-Schadt¹ & A.C. Frantz^{5,6 A} (2016): **Do cities represent sources, sinks or isolated islands for urban wild boar populations?** *Journal of Applied Ecology*

DOI: 10.1111/1365-2664.12756

M. Stillfried¹, K. Börner¹, F. Göritz⁷, J. Painer⁷, K. Röllig⁷, M. Wenzler^{1,8}, H. Hofer¹, S. Ortmann¹ and S. Kramer-Schadt¹: **Secrets of success in a landscape of fear: Urban wild boar use habitats that rural conspecifics avoid**

M. Stillfried¹, P. Gras¹, M. Busch^{1,9}, K. Börner¹, S. Kramer-Schadt¹, S. Ortmann¹ (submitted): **Wild inside: Urban dwelling wild boar select for natural food resources.**

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Acknowledgements

I would like to thank everyone who made this thesis possible:

Above all, I want to thank my supervisors Dr. Stephanie Kramer-Schadt and Dr. Sylvia Ortmann. You gave me the opportunity to grow up together with the wild boar project, thanks for your trust in me and all your technical and mental support during loops of enthusiasm-frustration - new ideas and motivation.

I am grateful to Prof. Dr. Heribert Hofer not only for evaluating the thesis, but also for giving me the opportunity to work at the IZW and for numerous constructive scientific discussions.

I am also thankful to Prof. Dr. Jörns Fickel for evaluating the thesis and for the constructive cooperation.

Thank you, Konstantin Börner, not only for your practical support but most of all for sharing numerous memories, happy moments of wild boar capture, freezing nights on the hunting stand and endless hours in the Hilux and going through (not always) inspiring conference experiences. Thanks also for introducing me into the world of hunters.

I would like to thank Dr. Frank Göritz, Dr. Johanna Painer and Dr. Kathleen Röllig for your professional work during wild boar anaesthesia and for the willingness for numerous stand-by hours. Many thanks also to Kathrin Schumann, Julia Bohner and Janina Radwainski.

I am grateful to Dr. Alain Frantz for the constructive cooperation and for convincing me that genetics can be fun.

Many thanks to Heidrun Barleben, Tanja Noventa, Ramona Taubert, Lia Hul and Doris Fichte for laboratory analyses and for tolerating all my smelly samples without complaining.

I am thankful to Dr. Anne Berger, Dr. Martin Dehnhard, Dr. Oliver Krone, Dr. Karin Müller and Prof. Dr. Katharina Jewegenow, Dr. Claudia Szentiks, Zoltan Mezöe and Dr. Gudrun Wibbelt for your cooperation and support.

Many thanks to Manuela Fischer, Matthias Maier, Sebastian Menke, Alexandre Courtiol and Ines Lesniak for your support in the field.

ACKNOWLEDGEMENTS

I would like to thank my office roommates for the great time, thank you, Robert Hagen Ilja Heckmann, Carolin Weh and Sophia Kimmig, it was a great pleasure to share the office, experiences, concerns and ideas with all of you.

Thanks to my interns Tim Borndoldt, Sabrina Paetzold, Erica Grant, Linda Bistere, Moritz Wenzler, Matthias Busch for their practical help, I enjoyed working with all of you.

Many thanks to my colleagues from the GIS Lab, the group coffee people, the lunch group and to the PhD students. I am grateful for the nice atmosphere and that I was able to meet so many interesting personalities.

I also thank Silke Ehle, Gabriele Liebich, Dagmar Boras, Beatrice Kehling, Stefanie Vollberg, Kathrin Hohnstädter and Wolfgang Tauche for your help, friendliness and patience with administrative work and Wolfgang Richter, Steffen Berthold and Knut Eichhorn for technical and practical support.

Ich bedanke mich bei den Berliner und Brandenburger Forsten, der Senatsverwaltung für Stadt und Umwelt Berlin und der Obersten Jagdbehörde Brandenburgs für die tatkräftige Unterstützung beim Fang von Wildschweinen, für die Beratung und die nötigen Genehmigungen: Danke Andreas Constien, dass du alles ins Rollen gebracht hast; danke Bodo Janitza, dass du so lange durchgehalten hast, auch wenn die Wildschweine nicht mitspielen wollten, danke Heiko Wessenberg für deinen kreativen Beitrag zur Namensgebung und für viele Stücke Kuchen; danke Uwe Peschke für deine endlose Geduld und Durchhaltevermögen; danke, Marion Schmolke nicht nur für die ganze Hilfe beim Fang sondern auch für den rührenden Einsatz für die Glienicker Wildschweine, danke an Andreas Burchardt, Arno Maximini, Lutz Wittich, Sabine Kopetzki. Vielen Dank an Derk Ehlert für die gemeinsame Wildschwein-Begeisterung und die stets positiven Worte über das Projekt.

Danke an Petra und Wolfgang Stillfried für die ganze Unterstützung bei allen Höhen und Tiefen, vielen Dank an meine Freunde und an Oliver März für deine Geduld, deinen tatkräftigen Beistand.

Finally I would like to thank the IZW for funding my position and the majority of the project. Many thanks also to the “Stiftung Naturschutz Berlin” and the National Geographic Society for additional funding.

Zusammenfassung

Die Ausdehnung urbaner Gebiete weltweit führt zu einer sinkenden Biodiversität, Habitat-Fragmentierung und –Verlust und damit zu einer großen Herausforderung für Wildtiere. Zum anderen gibt es aber auch Arten, die lernen, sich an die neuen Lebensräume anzupassen, in diesen bestehen und sogar erfolgreich sind. Selbst große Wildtiere gehören zu den so genannten „Urban Adapters“, die durch eine hohe Flexibilität ihres Verhaltensrepertoires in der Lage sind, mit den menschlichen Bewohnern von Großstädten zu koexistieren. Wie ihnen das gelingt, ist aber noch nicht verstanden, und vor allem über große, sozial lebende Säugetiere fehlen umfassende Untersuchungen, die die Urbanisierungsprozesse aus verschiedenen Blickwinkeln durchleuchten.

Wildschweine (*Sus scrofa*) sind soziale Wildtiere, deren Population weltweit wächst. Sie sind bekannt dafür, dass sie auch immer mehr in urbane Lebensräume vordringen, auch in die Stadt Berlin, was oft zu Konflikten führt. Berlin ist zu 20% mit Wäldern bedeckt, die in vier Forstgebiete unterteilt sind (Grünwald, Köpenick, Tegel, Pankow), und wird in den Medien immer wieder als Hauptstadt der Wildschweine bezeichnet, da die Wildschweine regelmäßig in Siedlungsgebiete der Menschen vordringen. Ob die Berliner „Siedlungsschweine“ Einwanderer aus dem Brandenburger Umland oder schon eigenständige, isolierte urbane Unter-Populationen sind, wie sie die urbanen Habitate nutzen und wovon sie sich ernähren, war bislang unbekannt und sollte durch die vorliegende Arbeit untersucht werden. Das Wildschwein ist ein geeignetes Modelltier, da gleichzeitig allgemeine ökologische Erkenntnisse über die Urbanisierung von Wildtieren und ortspezifische Erkenntnisse gewonnen werden können, die lokalen Behörden hilfreiche Einblicke ermöglichen, so dass das Projekt, welches im Rahmen dieser Doktorarbeit etabliert wurde, auf großes öffentliches Interesse gestoßen ist.

In **Manuskript 1 (Kapitel 2)** beschäftigte ich mich mit der Frage, ob Berliner Stadtwildschweine isolierte Populationen bilden oder ob zwischen Siedlungsschweinen und benachbarten urbanen und ruralen Waldschweinen eine sogenannte „Source-Sink-Dynamik“ besteht. Unter einer Source-Sink-Dynamik versteht man einen kontinuierlichen Strom aus einem qualitativ hochwertigen Lebensraum (=Source) mit hohem Populationszuwachs in qualitativ schlechtere Habitate (=Sink), in denen die Überlebensrate sinkt. Durch die Analyse von 13 Mikrosatelliten in der DNA von 365 adulten Wildschweinen, deren Proben auf Jagden

genommen wurden, konnte ich zeigen, dass in Berlin und Brandenburg insgesamt vier genetisch differenzierte Populationen existieren. Drei dieser Populationen sind in den Kerngebieten der Berliner Forstwälder Grunewald, Tegel und Köpenick zu finden, während Individuen aus dem vierten Forstgebiet Pankow gemeinsam mit den Brandenburger Wildschweinen die vierte Population bilden. Während die Stadtwald-Populationen aus Köpenick und dem Grunewald durch Gründertiere der Brandenburger Land-Population entstanden sind, stammt die Tegeler Stadtwald-Population von Tieren aus dem benachbarten Grunewald ab. Wildschweine, die innerhalb menschlicher Siedlungsräume beprobt wurden, stammen nicht wie erwartet aus den benachbarten Stadtwäldern, sondern von der Brandenburger Land-Population ab. Mit den Ergebnissen dieser ersten Teilstudie konnte ich also zeigen, dass in Berlin und Brandenburg isolierte Populationen in den Stadtwäldern vorkommen und gleichzeitig innerhalb der Berliner Stadtgrenzen und dem ländlichen Umland eine Source-Sink-Dynamik besteht. Gründe für die Isolation der Stadtwald-Populationen konnten durch die Analysen nicht belegt werden, allerdings lässt sich spekulieren, ob die Berliner Mauer, die die Grunewalder und Tegeler Population vom Umland abgeschnitten hat, die genetische Separierung dieser beiden Populationen begünstigt hat. Allerdings ist auch im Köpenicker Stadtwald, der nicht abgetrennt war, eine isolierte Population entstanden. Daher spielen Landschaftsstrukturen wie Straßen und Gewässer, die die isolierten Populationen umschließen, oder möglicherweise Unterschiede im Verhalten der Wildschweine eine große Rolle. Auf Grundlage unserer Ergebnisse habe ich den Behörden ein grenzübergreifendes Management empfohlen, welches weitere Untersuchungen beispielsweise zur Populationsdichte beinhaltet, um angewandte Maßnahmen auch evaluieren zu können.

In **Manuskript 2 (Kapitel 3)** beschäftige ich mich mit dem Raumverhalten der Wildschweine. Ich habe Bewegungsmuster und Habitatpräferenzen urbaner und ruraler Wildschweine verglichen und dabei einen besonderen Fokus auf die Frage gelegt, inwieweit Wildschweine zwischen Nahrungsaufnahme (Nahrungslandschaft) und dem Vermeiden von Störungen durch den Menschen (Gefahrenlandschaft) abwägen, also wie mit Risiko umgegangen wird. Dazu habe ich 11 Wildschweine in Berlin und Brandenburg gefangen, mit GPS-Halsbändern ausgestattet und so knapp 80.000 Aufenthaltsorte bestimmt. Die Fluchtdistanz urbaner Wildschweine ist im Durchschnitt um ein Drittel kürzer als bei ruralen Wildschweinen. Ich konnte zeigen, dass rurale Wildschweine größere Streifgebiete haben als urbane Wildschweine und dass diese Streifgebiete – im Gegensatz zu denen urbaner Wildschweine - mit zunehmender Anzahl von Häusern größer werden. Außerdem haben

urbane Wildschweine ihre Schlafplätze monatlich weniger weit verlagert als rurale Individuen. Bezüglich der Habitatnutzung innerhalb der Streifgebiete konnte ich zeigen, dass urbane Wildschweine Habitate zur Nahrungsaufnahme nutzen, die von ruralen Wildschweinen als Gefahrenlandschaft angesehen und vermieden werden. So wählen urbane Wildschweine beispielsweise tagsüber Schlafplätze in der Nähe von Straßen oder häufig frequentierten Badestellen (kalkulierbares Risiko) und gehen nachts in der Nähe von Häusern auf Nahrungssuche. Urbane Wildschweine nutzen aber auch natürliche Waldhabitate, so dass „rurales“ Verhalten in urbanen Wildschweinen beobachtet werden kann, und gleichzeitig zeigen einige rurale Wildschweine „urbane“ Verhaltensweisen und nutzen teilweise auch die Nähe zu Häusern während der Nahrungssuche im Sommer. Die Ergebnisse zeigen die hohe Flexibilität und Anpassungsfähigkeit der Wildschweine. Diese kann letztendlich auch die Voraussetzung und die treibende Kraft für das Erschließen neuer Lebensräume sein.

In **Manuskript 3 (Kapitel 4)** habe ich mich mit der Nahrung urbaner Wildschweine beschäftigt und dabei Unterschiede zwischen Gruppen unterschiedlicher Herkunft betrachtet. Makroskopische Untersuchungen von 265 Wildschweinmägen, bei Jagden erhoben, haben gezeigt, dass nur in 14 Mägen Nahrungsmittel aus potentieller anthropogener Quelle zu finden waren, so dass die Vermutung, Wildschweine in urbanen Gebieten würden vor allem menschliche Abfälle konsumieren, nicht bestätigt werden konnte. Die makroskopische Einteilung in fünf Magenkategorien haben erste Unterschiede zwischen den genetischen Gruppen gezeigt, da Wildschweine im Grunewald beispielsweise viele so genannte „Eichelmägen“ hatten, die in Köpenick gar nicht zu finden waren; dort war vorrangig der so genannte „Fasermagen“ zu finden. Der Energiegehalt der Mägen war im Grunewald signifikant höher als in Brandenburg und auch zwischen den Magenkategorien gab es signifikante Unterschiede. Der prozentuale Anteil von säureunlöslicher Asche, Protein, Stärke, Fett- und Fasergehalt war signifikant unterschiedlich in den Magenkategorien, so war beispielsweise in Eichelmägen besonders viel Fett, in Fasermägen vorrangig Protein und in Maismägen sehr viel Stärke zu finden. Signifikante Unterschiede waren bei der Zusammensetzung der Landschaft in den Gruppen zu beobachten. In der Stadt sind menschlich geprägte Landschaftsvariablen wie Prozent der Versiegelung, Anzahl von Häusern und Einwohnerzahl am stärksten ausgeprägt, während in Brandenburg neben Wald auch viele landwirtschaftliche Flächen und Grünflächen zu finden sind. In den Stadtwäldern sind weniger Grünflächen als in Brandenburg, aber durch die direkte Nähe zur Siedlung teilweise dennoch höhere Einwohnerdichten als in Brandenburg zu finden. Vor allem die

Landschaftsvariablen, die mit menschlichen Strukturen assoziiert sind, wie Prozent der Versiegelung, Häuserdichte und Bevölkerungsdichte wirken sich nur geringfügig auf den Energiegehalt und verschiedenste Nährstoffmengen aus. Allerdings konnte ein Zusammenhang zwischen Stärke und Landwirtschaft (steigende Stärkemenge), Grünland (sinkende Stärkemenge) und Koniferenwäldern (steigender Stärkegehalt) festgestellt werden. Der Anteil säureunlöslicher Asche sank mit zunehmender Menge an Landwirtschaft und der Proteingehalt sank bei steigender Menge von Koniferenwäldern. Die untersuchten Mageninhalte zeigen insgesamt, dass zwar keine Nahrungsquellen aus anthropogener Herkunft genutzt werden, dass aber trotzdem deutliche räumliche Unterschiede bezüglich der genutzten Nahrungsressourcen vorliegen.

Insgesamt konnte ich durch die Studie zeigen, dass sich urbane Wildschweine deutlich von ruralen Wildschweinen unterscheiden. Zum einen durch die genetische Isolation in den Stadtwäldern, zum anderen durch unterschiedliche Verhaltensweisen in Bezug auf menschliche Störungen. Auch wenn der Anteil anthropogen geprägter Nahrungsmittel in urbanen Gebieten ähnlich gering ist wie in ruralen Gebieten, müssen Wildschweine in Nähe zum Menschen zur optimalen Nahrungsaufnahme ihr Verhalten anpassen, zum Beispiel durch Toleranz von menschlich geprägten Landschaftsstrukturen und die Toleranz direkter Störungen durch menschliche Nähe. Die hohe Flexibilität des Verhaltensspektrums sowie eine hohe Lernfähigkeit spielen dabei eine entscheidende Rolle.

Summary

The worldwide spread of urban areas leads to habitat fragmentation, habitat loss and a decrease in biodiversity. At the same time, more and more species learn to adjust to novel urban environments and manage to succeed in those. Even large wildlife species belong to the so-called urban adapters which use their high behavioural flexibility to coexist with human inhabitants of metropolitan areas. There is still a huge lack of knowledge regarding the ecology of wildlife in urban areas especially in addressing different perspectives.

Wild boar (*Sus scrofa*) a social wildlife species with an increasing population density worldwide colonize more and more urban areas, including Berlin, which leads to human wildlife conflicts. Twenty percent of Berlin is covered with forests, subdivided into four main forestry areas (Grünwald, Köpenick, Pankow, Tegel). Because wild boar regularly enter urban settlements in Berlin, the city is regularly called “capital of the wild boar”. The aim of this thesis was to investigate whether these conflict wild boar from Berlin are invaders from the rural surroundings or if they already founded a separate urban group, how they use urban habitats and what they forage. The wild boar is an ideal model species, because it provides general ecological insight into urbanization by large social wildlife species as well as site-specific findings which can support the managements, so that the project which was established during this thesis was of a broad public interest.

In **Manuscript 1 (Chapter 2)**, I investigated whether wild boar from the city of Berlin form isolated urban groups or if there is a „source-sink-dynamic“, linking neighbouring rural and urban areas. A Source-sink dynamic exists when individuals from a high quality source habitat with a high population growth disperse into sink habitats with a poor quality and a population decline. By analysing 13 microsatellite loci within the DNA of 365 adult and subadult hunted wild boar, I was able to show the existence of four genetically distinct populations in Berlin and Brandenburg. Three of those populations occurred in the core areas of the urban forests Grünwald, Tegel and Köpenick, while all remaining individuals from the rural areas of Brandenburg and the fourth urban forest Pankow formed the fourth population. While the urban forest populations from Köpenick and the Grünwald were founded by rural dispersers from Brandenburg, the third urban forest population in Tegel originated from the neighbouring urban population from the forest Grünwald. Wild boar, which were hunted within the city of Berlin did not as expected origin from the neighbouring urban forests, but from the rural population.

With help of the results of this first sub-study, I was able to show, that genetically isolated groups exist in the urban forest and at the same time that a sink-source dynamic exists between rural areas and Berlin city. My analyses did not give insights into reasons for the isolated groups but it is reasonable to assume, that the Berlin Wall which separated the Grunewald and Tegel forest played a role during the isolation process. But because another colonization and isolation took place within the urban Koenigswald forest, which was not separated, other factors, such as landscape variables or the behaviour of wild boar might have played another important role. Based on the results of the study, I suggested a common management for urban and rural wild boar populations and further investigations which should for example focus on population density to allow an evaluation of applied management methods.

In **Manuscript 2 (Chapter 3)**, I studied space use of wild boar. I compared space use and habitat preferences of urban and rural wild boar regarding the question, how wild boar manage to trade-off between energy intake (landscape of food) and human induced disturbance (landscape of fear). Therefore I caught 11 wild boar in Berlin and Brandenburg, equipped them with GPS-collars and collected about 80,000 wild boar locations. I was able to show, that the flight distance of urban wild boar is about one third shorter than that for rural wild boar. Further, I discovered that in comparison to urban wild boar, home ranges of rural wild boar are larger and increase with increasing percentage of houses. Urban wild boar shifted their resting sites less often than rural individuals. Regarding the habitat use, urban wild boar used the landscape of fear which was avoided by rural wild boar. They selected areas close to roads or frequently used bathing sites (both with a predictable risk) as resting sites and foraged close to houses at night. But urban wild boar also used natural forest habitats, so that “rural” behaviour was observed in urban wild boar and “urban” behaviour was observed in rural wild boar which occasionally foraged close to houses in summer. This shows the high behavioural plasticity of wild boar, which might function as driver for the colonization of novel habitats.

In **Manuscript (Chapter 4)**, I examined foraging characteristics of urban wild boar with a special focus on differences between groups of different origin. Macroscopic analyses of 265 wild boar stomachs which were collected from hunted animals revealed that only 15 of the stomach contents contained subjects from potential anthropogenic origin, so I had to reject the assumption that wild boar enter urban areas in order to consume human garbage. A grouping of stomachs into macroscopic categories due to the most dominant content presented first differences between groups of different origin: Wild boar from the urban Grunewald forest for

example had mostly so called "acorn-stomachs", while those were absent in individuals from the Koepenick forest, where the so called "fibre-stomach" was most dominant among wild boar. The amount of energy of the stomach contents was significantly higher in individuals from the Grunewald forest and within acorn stomachs. Starch was especially high in Maize-stomachs, fat in acorn-stomachs and protein in fibre stomachs. The landscape varied among the wild boar groups. Within the city of Berlin, human associated landscape variables such as percentage of sealed ground and houses as well as human population density are most dominant while the rural area in Brandenburg is formed by forests and agricultural areas. The urban forests contain almost no agricultural and greenland areas but a relatively high human population density and percentage of houses due to the nearby city. Landscape structures which are associated with humans, such as percentage of sealed ground and houses as well as human density played a minor role for nutrient variables. However I found a correlation between the amount of starch and agriculture (starch increasing), greenland (starch decreasing) and coniferous forests (starch increasing). The percentage of acid insoluble ash decreased with increasing percentage of agriculture and the percentage of protein decreased with increasing percentage of coniferous forests. The stomach content analysis revealed that human associated food sources are not predominantly used and demonstrates spatial differences regarding food resources used.

In summary I was able to show with my study that urban and rural wild boar differ not only because of a genetic isolation within the urban forests but also due to novel behaviour towards human induced disturbances. Even if the amount of anthropogenic food sources is low in both urban and rural areas, wild boar have to adjust their space use and behaviour to be able to succeed in a human dominated landscape. The high behavioural flexibility and learning ability might thereby function as driver for urban adjustment.

CHAPTER 1: General Introduction

1.1. URBANIZATION AND URBAN (WILDLIFE) ADAPTERS

Urban land expansion rates and urban population growth rates are increasing worldwide, leading to a fragmentation of habitats and endangering biodiversity (Seto *et al.* 2011). Wildlife differs in the ability to adapt to environmental changes associated with urbanization (Blair 1996). While ‘urban avoiders’ are sensitive to human persecution and habitat disturbance, ‘urban adapters’ or ‘edge species’ occur in the matrix of human land uses including agriculture, villages and cities, often in suburbs whereas the ‘urban exploiters’, often called synanthrophs, even depend on human resources (Blair 1996; McKinney 2002). This concept and the terminology, which was first introduced by Blair and further developed by McKinney, was again modified by Fischer (Fischer *et al.* 2015), based on population dynamics in developed (substantially altered for residential, recreational, commercial, or industrial purposes) vs. natural areas (minimally modified for human use). In his concept urban avoider populations can be extirpated in developed landscapes but occur in natural areas embedded in an urban matrix. Urban utilizers range from occasional use of urban resources to breeding in developed areas. Urban dwellers vary from having viable populations in both natural and developed areas to being entirely dependent on developed areas for survival.

The aim of my thesis was to investigate the concept of urban dwellers/ utilizers across scales, from coarse-scale to small-scale, using different state-of-the-art techniques. As model species I chose wild boar (*Sus scrofa*), which is characterized by worldwide population increase (Sáez-Royuela & Telleria 1986; Bieber & Ruf 2005; Massei *et al.* 2015; Keuling, Strauss & Siebert 2016) and a high behavioural plasticity which allows the species to adjust to altering conditions (Dardaillon 1986; Keuling, Stier & Roth 2009; Servanty *et al.* 2009; Ohashi *et al.* 2013; Podgorski *et al.* 2013). In addition, (I) studies on large social mammals are rare, (II) wild boar inhabit rural and urban habitats, and (III) often get into conflicts with humans and are therefore of broad interest. The analysis of spread and dispersal with help of genetic methods gives insights into coarse, population scale ecological adjustment to urban environments. This has previously been shown on a coarse scale in urban fox (*Vulpes vulpes*) in Zürich (Gloor *et al.* 2001; Wandeler *et al.* 2003), which form isolated urban sub-populations.

Analysing habitat use within urban areas with help of GPS-telemetry gives an understanding of ecological adjustment of urban dwellers and utilizers on the intermediate, regional scale. Home range size, for example, will most likely not be static but will vary seasonally, as demonstrated in urban dwelling coyotes (*Canis latrans*) showing a high seasonal variability in some cities (Grinder & Krausman 2001).

A small-scaled, local approach characterizes habitat use on a detailed level, e.g. by studying foraging characteristics, food choice and selectivity within the home range of urban dwellers and utilizers. The range of including anthropogenic food into the diet varies from “occasionally” in Black bears (*Ursus americanus*) in urban areas (Merkle *et al.* 2013; Lewis *et al.* 2015) to direct feeding by humans in urban Formosan Macaques (*Macaca cyclopis*) and wild boar (Kotulski & König 2008; Hsu, Kao & Agoramoorthy 2009; Cahill *et al.* 2012). In the following, I will elaborate on the concepts arising at different scales, starting with the coarse scale which leads to an ecological understanding on the population level.

1.2. COARSE SCALE POPULATION STRUCTURE - SOURCES, SINKS AND ISOLATED ISLANDS

Urbanization processes on a coarse, population scale can be influenced by different dynamics including an animal’s decision to select specific habitats (Dill 1987; Lima & Dill 1990; Lima 1998; Chittka, Skorupski & Raine 2009), as well as pressure and limiting factors of habitat resources and structures. While urban utilizers range from occasional use of urban resources to breeding in developed areas, urban dwellers vary from having viable populations in both natural and developed areas to being entirely dependent on developed areas for survival (Fischer *et al.* 2015). To understand underlying processes, it is necessary to study whether urban populations were founded by a few dispersers and are isolated such as described by the urban island hypothesis (Gloor *et al.* 2001; Wandeler *et al.* 2003) or if there is a source-sink-dynamic between urban and rural habitats (Pulliam 1988). This would mean, that a high quality habitat allowing for high birth rates and low mortality and therefore with a net population increase functions as source for a low quality sink habitat with lower birth rate and high mortality and a net population decline (Pulliam 1988; Dias 1996). Areas with a high abundance of resources and a population density below carrying capacity (due to high human induced mortality) can act as attractive sinks (even though they are ecological “sinks”), which

is also a likely scenario for urban areas (Delibes, Ferreras & Gaona 2001; Naves *et al.* 2003). Because individual habitat choice is a key process underlying source–sink dynamics (Delibes, Ferreras & Gaona 2001), population genetic analyses can give first insights into the quality of urban habitats. Further insights into the quality of urban habitats can be revealed by detailed analyses of resource availability in a landscape and an analysis which habitats are selected by animals.

1.3. INTERMEDIATE TO SMALL SCALES OF HOME RANGE ESTABLISHMENT AND RESOURCE SELECTION - THE TRADE-OFF BETWEEN FORAGE AND FEAR IN URBAN AREAS

Cities can provide an attractive foraging landscape, including anthropogenic, easily accessible food sources such as garbage, pet food or wildlife feeding (Cahill *et al.* 2012; Murray *et al.* 2015; Theimer *et al.* 2015; Tryjanowski *et al.* 2015). These food sources are often easily accessible and contain a high amount of energy (Ottoni, de Oliveira & Young 2009; Maibeche *et al.* 2015). In addition, green areas in cities are often rich in plant and animal biodiversity (Beninde, Veith & Hochkirch 2015) and might provide attractive natural food. Street trees or forest patches are common in most cities (Nowak *et al.* 2001; Pauleit *et al.* 2002) and their products provide another natural food source within the urban foraging landscape.

To enhance usage of these high quality resources animals have to optimize foraging in the urban environment. The underlying concept of optimal foraging (OFT) is described by different models (Emlen 1966; MacArthur & Pianka 1966; Charnov 1976; Pyke, Pulliam & Charnov 1977; Krebs 1978; Pyke 1984) and is shaped by the following main characteristics:

- (1) type of food choice, as food differs with respect to caloric value and consumption/processing time (Emlen 1966; Pyke, Pulliam & Charnov 1977);
- (2) optimal patch choice, because food availability is not homogenously distributed within the landscape (MacArthur & Pianka 1966; Charnov 1976; Pyke, Pulliam & Charnov 1977);
- (3) optimal allocation of time spent in different patches (Pyke, Pulliam & Charnov 1977);
- (4) optimal pattern and speed of movement between patches (Pyke, Pulliam & Charnov 1977).

Optimal foraging theory includes a heritable component of foraging behaviour which can be either the actual foraging responses or the rules by which an animal learns to make such responses. Animals usually have offspring which forages in the same manner, therefore the proportion of individuals in a population, which forage in a way to optimize their fitness is expected to increase over time (Pyke 1984). For the coarse scaled ecological approach this includes that - although each individual has to make foraging decisions itself - typical foraging patterns might be a population-wide phenomenon. Due to this theoretical construct, I considered for the intermediate and small scale analyses that patches with optimal foraging conditions can be defined as landscape of food, which is probably different in urban and rural landscapes. Urban developed landscapes, as described above might provide additional high energy human associated food sources (Fig. 1.1, Cahill *et al.* 2012; Murray *et al.* 2015; Theimer *et al.* 2015; Tryjanowski *et al.* 2015, Ottoni, de Oliveira & Young 2009; Maibeche *et al.* 2015) whereas the forage landscape in rural areas is probably characterized by natural food sources and agricultural crops and only a small percentage of human associated food sources such as garbage and direct feeding (Fig. 1.1, Conover & Decker 1991; Naughton-Treves *et al.* 1998; Schley & Roper 2003; Amici *et al.* 2012; Nasiadka & Janiszewski 2015).

However, OFT had been criticised for various reasons (Pierce & Ollason 1987), with the most critical point being that foraging animals are not free in their decisions, they have to consider predator-induced threats, including disturbance by humans (Brown, Laundre & Gurung 1999; Frid & Dill 2002), i.e. their decisions are also embedded in a landscape of fear. Disturbance stimuli and human disturbance in particular are analogous to predation risk and impact the individual's behaviour on different levels. Numerous studies proved and investigated the direct and indirect impact of humans on

1. predator induced flight initiation distance (the distance between the predator and prey at which prey begin to flee; Heidiger 1934; Walther 1969; Frid & Dill 2002);
2. vigilance (Dyck & Baydack 2004; Benhaiem *et al.* 2008; Jayakody *et al.* 2008; Sönnichsen *et al.* 2013)
3. habitat selection and movement patterns (Bechet, Giroux & Gauthier 2004; Graham *et al.* 2009; Stillfried *et al.* 2015).
4. energy intake and reproductive success, having indirect impacts at the population level (Frid & Dill 2002; Ciuti *et al.* 2012).

Disturbance stimuli, just like food items, are often related to specific patches, by this creating a landscape of fear (Laundre J. W., Hernandez L. & Ripple W. J. 2010; Ciuti *et al.* 2012; Laundre *et al.* 2014; Rosner *et al.* 2014; Schmidt & Kuijper 2015; Stoen *et al.* 2015). Free ranging animals are able to distinguish between spatial variations in risk (Bonnot *et al.* 2013; Rosner *et al.* 2014; Stillfried *et al.* 2015) and deal with it. The landscape of fear represents relative levels of predation risk as peaks and valleys reflecting the level of fear in time and space (Hernández & Laundré 2005; Laundre J. W., Hernandez L. & Ripple W. J. 2010).

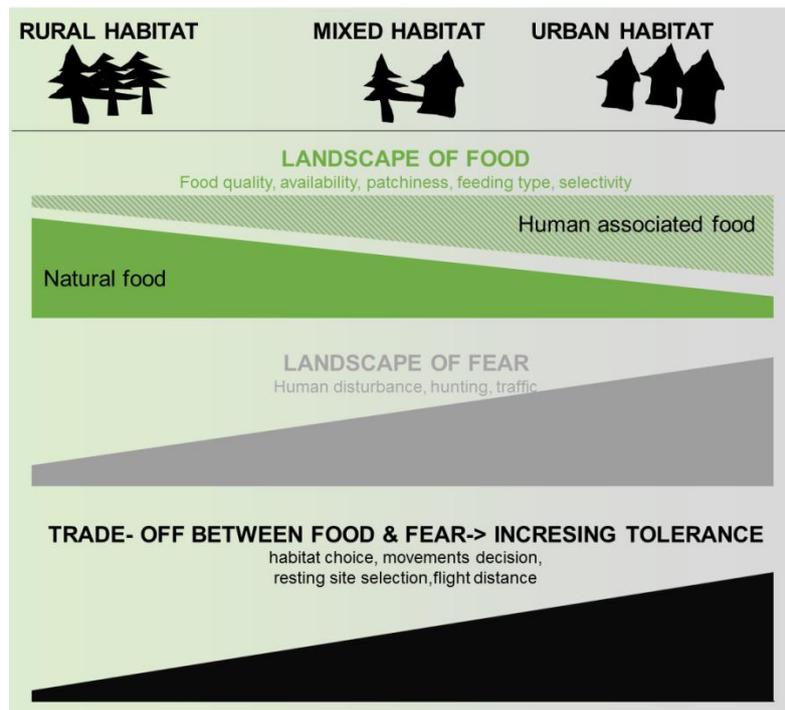


Fig. 1.1: Conceptual framework to describe an animal decision's trade-off between the landscape of food and the landscape of fear along the rural-urban habitat gradient.

The landscape of fear and how animals respond to it in an urban context had not yet been studied. I expect the landscape of fear to increase in cities due to the high human density (Fig. 1.1), the high traffic volume and additional predators such as pets, providing increased disturbance and mortality risk for urban animals (Frid & Dill 2002; Baker *et al.* 2005; Hughes & Macdonald 2013). Permanent avoidance behaviour is cost intensive (Frid & Dill 2002), thus any decision will be a trade-off between the risk/disturbance and the benefits to be gained from engaging in a given activity (Lima & Dill 1990). For urban animals this can mean that they adjust to the presence of humans, become more tolerant towards disturbances and therefore modulate their perception of the landscape of fear (Fig. 1.1). Habitat selection

studies have the power to answer questions about the impact of habitat characteristics on modulations of the landscape of fear at different spatial scales.

1.4. JOHNSON'S HABITAT SELECTION ORDERS AND VARIABLES OF INTEREST

The adjustment of animals to urban environments is a function of the requirements of the animal and the characteristics/variability of the habitat, and therefore the analysis of adjustment needs to distinguish between availability of resources within the landscape and usage by the animal (Johnson 1980). Resource use and preference should therefore be investigated on different hierarchical habitat selection orders (Johnson 1980): The first order selection is the geographical or physical range of the species, the second order determines the home range establishment and the third order pertains to the usage made of various habitat components within the home range. If the third order is a feeding site, food items chosen within that patch can be the fourth order. Abundance of a component (= the component's quantity), the availability (= accessibility), the usage (= quantity of the component in a fixed period of time), the selection (= use in disproportion to availability) and the preference (= likelihood that a consumer will choose the component) can be differentiated in this context (Johnson 1980).

In my thesis, I analysed across all habitat selection orders, how urban dwellers/utilizers adapt to novel urban environments using telemetry methods and in consideration how animals trade-off between the natural and human induced landscape of food and the landscape of fear which is especially relevant in urban areas. Several previous studies focussed on one of the described habitat selection orders, but an integrating study on urban wildlife from the coarse to small scale is still missing and considered necessary.

1.5. THE WILD BOAR MODEL (=BERLIN'S WILD BOAR) AND WORKING HYPOTHESES

Studies on urban mammals are often conducted with medium-sized mammals such as foxes, badgers (*Meles meles*) or coyotes (Gloor *et al.* 2001; Grinder & Krausman 2001; Davison *et al.* 2008; Gehrt, Anchor & White 2009), but studies on large social mammals in urban areas are rare. Wild boar (*Sus scrofa*) are social mammals with a growing population throughout Europe (Massei *et al.* 2015; Keuling, Strauss & Siebert 2016) and an increased presence in

urban areas (Dinter 1991; Cahill, Llimona & Gracia 2003; Jansen *et al.* 2007; Cahill *et al.* 2012; Podgorski *et al.* 2013). Wild boar are frequently in conflict with people because they are potential transmitters of zoonotic diseases or diseases relevant to livestock (Fernández, Kramer-Schadt & Thulke 2006; Jansen *et al.* 2007; Chiari *et al.* 2015) and because they can destroy agricultural crops and therefore could be responsible for economic damage (Amici *et al.* 2012; Ficetola *et al.* 2014; Jarolimek *et al.* 2014; Laznik & Trdan 2014).

Thus, wild boar are a very useful model species to study the ecological adaptations of urban avoiders, utilizers and dwellers (Fischer *et al.* 2015) on different scales and selection orders, thereby assisting local authorities in developing appropriate management tools to minimise potential wildlife-human conflict.

In contrast to numerous studies on wild boar home range size and movement kinetics in natural and agricultural landscapes (Dardaillon & Beugnon 1987; Cousse *et al.* 1992; Janeau *et al.* 1995; Thurffjell, Spong & Ericsson 2013; Jarolimek *et al.* 2014; Morelle, Lehaire & Lejeune 2014; Morelle *et al.* 2015), detailed knowledge about urban wild boar ecology is rare (Dinter 1991; Cahill, Llimona & Gracia 2003; Jansen *et al.* 2007; Kotulski & König 2008; Cahill *et al.* 2012; Podgorski *et al.* 2013) and only specific questions are addressed. However, it has been shown that urban wild boar from the Collserola Park in Barcelona (Cahill, Llimona & Gracia 2003) became habituated to humans (because of direct feeding) especially in the hot and dry summer months when foraging conditions in the forests are poor in Spain. Urban wild boar in Krakow, Poland, had smaller home ranges but needed to travel twice as much as rural wild boar to cover their energy requirements within the patchy urban environment (Podgorski *et al.* 2013).

Wild boar in Berlin and the neighbouring Federal State Brandenburg seem to differ regarding their tolerance towards humans and their habitat use. Rural wild boar from Brandenburg can easily be tracked with wildlife cameras (Fig. 1.2), but direct observations are rare, and I therefore consider them as being urban avoiders. Their habitat is characterized by large forests mainly dominated by pine (*Pinus silvestris*) monocultures. These forests are interspersed with small villages and large agricultural fields with a high percentage of rye (*Secale cereale*) and increasingly maize (*Zea mais*) and rape (*Brassica napus*, personal observations and documentations during field work).

Two behavioural phenotypes of wild boar are common in Berlin: Urban forest wild boar occur in the four large urban forest areas of Berlin (Grunewald, Tegel, Koepenick and

Pankow) and are easily to monitor even during the day (Fig. 1.2). These forests cover 20% of the area of Berlin and the forest edges border urban settlements. While the eastern forests (Koenig and Pankow) are similar in their structure to typical Brandenburg pine forests, the western forests are more admixed and contain also a high percentage of deciduous trees such as oak (*Quercus spec.*, Berlin 2015, personal observations). Urban forest wild boar are classified as urban utilizers. Wild boar also often occur in settled and occupied parts of the city (= city wild boar, Fig. 1.2) and can be considered as urban dwellers or utilizers. These wild boar come into conflict with humans, and specialized city hunters were trained since 2000 to shoot wild boar within the urban settlements, leading to a hunting pressure in urban areas similar or even higher than in rural areas (Hespeler 2007; Kopetzki 2016). Many newspaper articles and television documentaries spread the common opinion that wild boar from the rural and urban forests invade the city in order to consume human garbage or receive direct feeding, but scientific data were still missing until the onset of this study.

1.6. OBJECTIVES OF THE THESIS

The overarching aim of my thesis was to characterize behavioural mechanisms enabling wild boar to adjust to urban environments. This involves proving hypotheses (urban areas as sources, sinks or isolated islands, trade-off between the landscapes of food and fear) on different habitat selection orders and across scales.

For the coarse scale (alternative approach to Johnson's first selection order, the range of the wild boar, **Manuscript 1 (Chapter 2)**), I hypothesized, that human dominated urban habitats lead to a genetic differentiation between wild boar from Berlin and Brandenburg. I predicted that city wild boar are driven into settlements from overpopulated neighbouring urban forests.

Using genetic analyses of microsatellites, I aimed

- (1) to analyse the population genetic structure of Berlin and the neighbouring Brandenburg
- (2) to reconstruct the colonization history of the detected clusters and
- (3) to determine the genetic origin of the so-called city wild boar which were not included into the above mentioned clustering method.

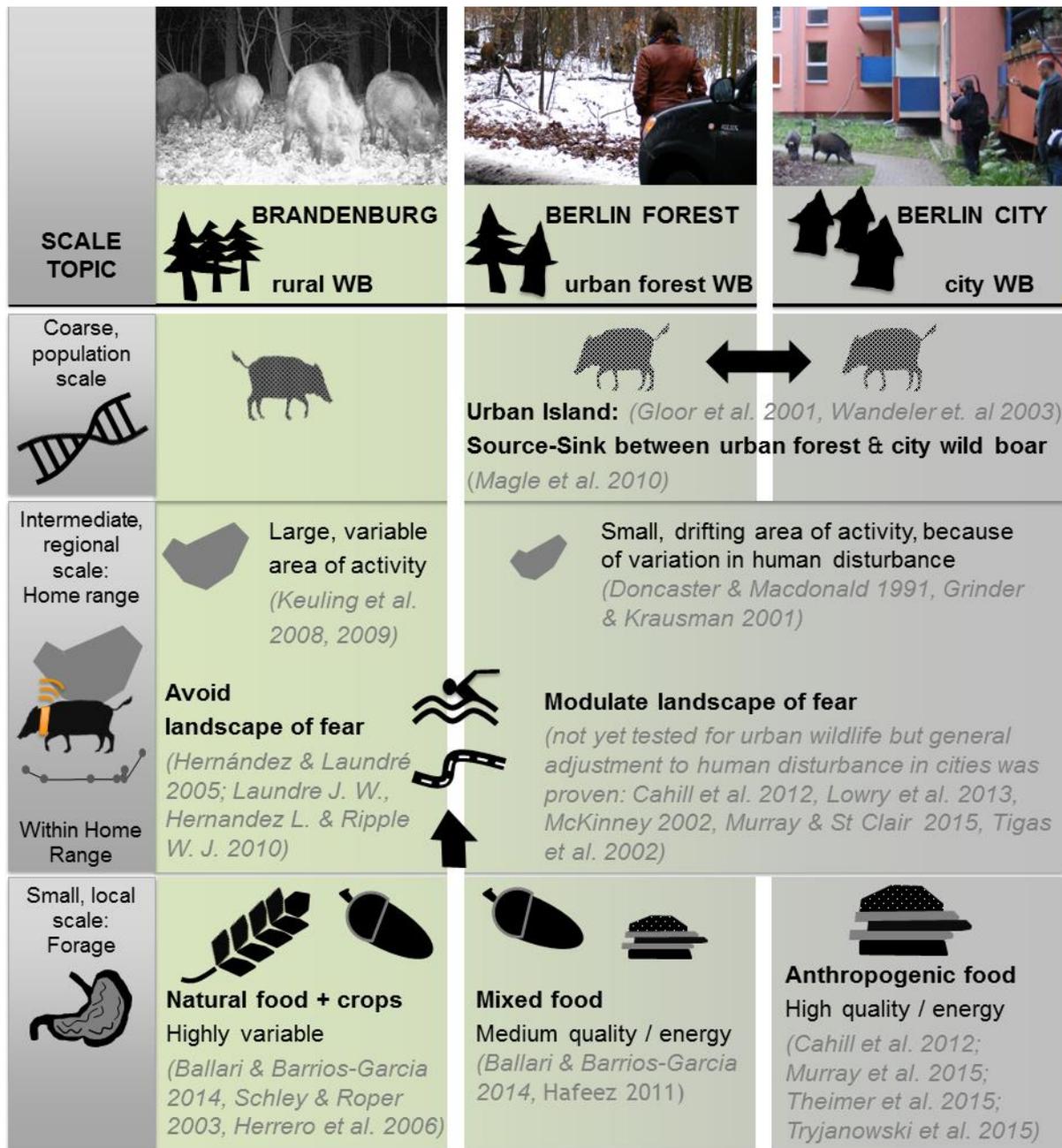


Fig. 1.2: Predictions for the behavioural adjustment of wild boar (abbreviated as WB) to urban areas among scales. Three types of wild boar are considered: Rural wild boar occur in natural rural environments and are difficult to be observed. Urban forest wild boar are those which can be easily approached within urban forests, and city wild boar occur within the urban area of Berlin. Based on the literature, I formulated predictions on a coarse to small scale, which are displayed in the Fig. in a simplified way.

On the regional scale (second and third habitat selection order: home range level and within homerange level, **Manuscript 2 (Chapter 3)**) I hypothesized that wild boar in urban environments adjusted their perception of risk, i.e. modulated their landscape of fear, in order to find sufficient food and shelter in a novel environment. I predicted that the trade-off

between fear and food will be biased in favour of food, if the potential rewards in the urban environment are higher than in the rural one. This requires modulation of the landscape of fear rather than modulation of the landscape of food. Using fine scaled telemetry data, I aimed to test if

- (1) urban wild boar have smaller home ranges due to a rich diet, and if they have to shift their home range more often than rural wild boar in response to the human-induced landscape of fear;
- (2) within the home range, urban wild boar have to adjust to the landscape of fear on a spatial scale by selecting landscape elements with a decreased or predictable disturbance;
- (3) in order to avoid humans, urban wild boar have to adjust to human activity and modulate their behaviour not only on a spatial but also on temporal (daily and seasonal) scale.

On the fourth habitat selection order (forage at a specific habitat, **Manuscript 3 (Chapter 4)**), I hypothesized that the diet of wild boar differs among rural Brandenburg, in urban forests of Berlin and in Berlin city. I predicted that wild boar in the city of Berlin have access to food sources with a higher quality. By macroscopic and nutritional analysis of wild boar stomachs, I aimed to investigate whether

- (1) the amount of anthropogenic food sources is highest in stomachs of wild boar from urban Berlin and if different macroscopic stomach content types differ in their composition of visible contents;
- (2) different macroscopic stomach content types equally frequent within different origins;
- (3) the percentage of either human, forest or agriculturally dominated landscape variables differs among origins
- (4) landscape structures within origins influence energy and food quality.

Finally, in **Chapter 5** I summarize the key findings of the thesis and discuss them in a broader context of urban wildlife species. The Appendix, **Chapter 6** contains four parts: To support my general discussion of the thesis, I include some supplementary data which are presented and explained in the appendix **Chapter 6.1**. The appendix contains also supplementary information for the three manuscripts (**Chapter 6.2-6.4**).

1.7. REFERENCES

- Amici, A., Serrani, F., Rossi, C.M. & Primi, R. (2012) Increase in crop damage caused by wild boar (*Sus scrofa* L.): the "refuge effect". *Agronomy for Sustainable Development*, **32**, 683-692.
- Baker, P.J., Bentley, A.J., Ansell, R.J. & Harris, S. (2005) Impact of predation by domestic cats *Felis catus* in an urban area. *Mammal Review*, **35**, 302-312.
- Ballari, S.A. & Barrios-Garcia, M.N. (2014) A review of wild boar *Sus scrofa* diet and factors affecting food selection in native and introduced ranges. *Mammal Review*, **44**, 124-134.
- Bechet, A., Giroux, J.-F. & Gauthier, G. (2004) The effects of disturbance on behaviour, habitat use and energy of spring staging snow geese. *Journal of Applied Ecology*, **41**, 689-700.
- Benhaiem, S., Delon, M., Lourtet, B., Cargnelutti, B., Aulagnier, S., Hewison, A.M., Morellet, N. & Verheyden, H. (2008) Hunting increases vigilance levels in roe deer and modifies feeding site selection. *Animal Behaviour*, **76**, 611-618.
- Beninde, J., Veith, M. & Hochkirch, A. (2015) Biodiversity in cities needs space: a meta-analysis of factors determining intra-urban biodiversity variation. *Ecology Letters*, **18**, 581-592.
- Berlin, S.f.S.u.U. (2015) Alters und Bestandsstruktur der Wälder www.stadtentwicklung.berlin.de/umwelt/umweltatlas/e_text/kb504.doc.
- Bieber, C. & Ruf, T. (2005) Population dynamics in wild boar *Sus scrofa*: ecology, elasticity of growth rate and implications for the management of pulsed resource consumers. *Journal of Applied Ecology*, **42**, 1203-1213.
- Blair, R.B. (1996) Land use and avian species diversity along an urban gradient. *Ecological Applications*, **6**, 506-519.
- Bonnot, N., Morellet, N., Verheyden, H., Cargnelutti, B., Lourtet, B., Klein, F. & Hewison, A.J.M. (2013) Habitat use under predation risk: hunting, roads and human dwellings influence the spatial behaviour of roe deer. *European Journal of Wildlife Research*, **59**, 185-193.
- Brown, J.S., Laundre, J.W. & Gurung, M. (1999) The ecology of fear: Optimal foraging, game theory, and trophic interactions. *Journal of Mammalogy*, **80**, 385-399.
- Cahill, S., Llimona, F., Cabaneros, L. & Calomardo, F. (2012) Characteristics of wild boar (*Sus scrofa*) habituation to urban areas in the Collserola Natural Park (Barcelona) and comparison with other locations. *Animal Biodiversity and Conservation*, **35**, 221-233.
- Cahill, S., Llimona, F. & Gracia, J. (2003) Spacing and nocturnal activity of wild boar *Sus scrofa* in a Mediterranean metropolitan park. *Wildlife Biology*, **9**, 3-13.
- Charnov, E.L. (1976) Optimal foraging, the marginal value theorem. *Theoretical Population Biology*, **9**, 129-136.
- Chiari, M., Ferrari, N., Bertolotti, M., Avisani, D., Cerioli, M., Zanoni, M., Alborali, L.G., Lanfranchi, P., Lelli, D., Martin, A.M. & Antonio, L. (2015) Long-Term Surveillance of Aujeszky's Disease in the Alpine Wild Boar (*Sus scrofa*). *Ecohealth*, **12**, 563-570.
- Chittka, L., Skorupski, P. & Raine, N.E. (2009) Speed-accuracy tradeoffs in animal decision making. *Trends in Ecology & Evolution*, **24**, 400-407.
- Ciuti, S., Northrup, J.M., Muhly, T.B., Simi, S., Musiani, M., Pitt, J.A. & Boyce, M.S. (2012) Effects of Humans on Behaviour of Wildlife Exceed Those of Natural Predators in a Landscape of Fear. *Plos One*, **7**, 13.
- Conover, M.R. & Decker, D.J. (1991) Wildlife damage to crops - perceptions of agricultural and wildlife professionals in 1957 and 1987. *Wildlife Society Bulletin*, **19**, 46-52.
- Cousse, S., Janeau, G., Spitz, F., Priede, I.G. & Swift, S.M. (1992) Telemetry on free-ranging wild boars (*Sus scrofa* L.): temporal and spatial structure of daily movements. *Priede IG & Swift SM, Edits. Wildlife telemetry. London: Ellis Horwood (1992): 693-697.*
- Dardaillon, M. (1986) Seasonal variations in habitat selection and spatial distribution of wild boar (*Sus scrofa*) in the Camargue, Southern France. *Behavioural Processes*, **13**, 251-268.
- Dardaillon, M. & Beugnon, G. (1987) The influence of some environmental characteristics on the movements of wild boar *Sus-scrofa*. *Biology of Behaviour*, **12**, 82-92.
- Davison, J., Huck, M., Delahay, R.J. & Roper, T.J. (2008) Urban badger setts: characteristics, patterns of use and management implications. *Journal of Zoology*, **275**, 190-200.

- Delibes, M., Ferreras, P. & Gaona, P. (2001) Attractive sinks, or how individual behavioural decisions determine source-sink dynamics. *Ecology Letters*, **4**, 401-403.
- Dias, P.C. (1996) Sources and sinks in population biology. *Trends in Ecology & Evolution*, **11**, 326-330.
- Dill, L.M. (1987) Animal decision making and its ecological consequences: the future of aquatic ecology and behaviour. *Canadian Journal of Zoology*, **65**, 803-811.
- Dinter, U. (1991) Das Raum-Zeitverhalten von Schwarzwild im Grunewald in den Sommermonaten unter besonderer Berücksichtigung menschlicher Störungen, Dissertation, Ludwig-Maximilians-Universität
- Doncaster, C.P. & Macdonald, D.W. (1991) drifting territoriality in the red fox *Vulpes-vulpes*. *Journal of Animal Ecology*, **60**, 423-439.
- Dyck, M.G. & Baydack, R.K. (2004) Vigilance behaviour of polar bears (*Ursus maritimus*) in the context of wildlife-viewing activities at Churchill, Manitoba, Canada. *Biological Conservation*, **116**, 343-350.
- Emlen, J.M. (1966) The role of time and energy in food preference. *American Naturalist*, **100**, 611-617.
- Fernández, N., Kramer-Schadt, S. & Thulke, H.-H. (2006) Viability and risk assessment in species restoration: planning reintroductions for the wild boar, a potential disease reservoir, *Ecology and Society* **11.1**
- Ficetola, G.F., Bonardi, A., Mairota, P., Leronni, V. & Padoa-Schioppa, E. (2014) Predicting wild boar damages to croplands in a mosaic of agricultural and natural areas. *Current Zoology*, **60**, 170-179.
- Fischer, J.D., Schneider, S.C., Ahlers, A.A. & Miller, J.R. (2015) Categorizing wildlife responses to urbanization and conservation implications of terminology. *Conservation Biology*, **29**, 1246-1248.
- Frid, A. & Dill, L. (2002) Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology*, **6** (1):11.
- Gehrt, S.D., Anchor, C. & White, L.A. (2009) Home range and landscape use of coyotes in a metropolitan landscape: conflict or coexistence? *Journal of Mammalogy*, **90**, 1045-1057.
- Gloor, S., Bontadina, F., Hegglin, D., Deplazes, P. & Breitenmoser, U. (2001) The rise of urban fox populations in Switzerland. *Mammalian Biology*, **66**, 155-164.
- Graham, M.D., Douglas-Hamilton, I., Adams, W.M. & Lee, P.C. (2009) The movement of African elephants in a human-dominated land-use mosaic. *Animal Conservation*, **12**, 445-455.
- Grinder, M.I. & Krausman, P.R. (2001) Home range, habitat use, and nocturnal activity of coyotes in an urban environment. *Journal of Wildlife Management*, **65**, 887-898.
- Hafeez, S., Abbas, M., Khan, Z.H. & Rehman, E.U. (2011) Preliminary analysis of the diet of wild boar (*Sus scrofa* L., 1758) in Islamabad, Pakistan. *Turkish Journal of Zoology*, **35**, 115-118.
- Heidiger, H. (1934) Zur Biologie und Psychologie der Flucht bei Tieren. *Biologisches Zentralblatt*.
- Hernández, L. & Landré, J.W. (2005) Foraging in the 'landscape of fear' and its implications for habitat use and diet quality of elk *Cervus elaphus* and bison *Bison bison*. *Wildlife Biology*, **11**, 215-220.
- Herrero, J., García-Serrano, A., Couto, S., Ortuño, V.M. & García-González, R. (2006) Diet of wild boar *Sus scrofa* L. and crop damage in an intensive agroecosystem. *European Journal of Wildlife Research*, **52**, 245-250.
- Hespeler, B. (2007) Leitlinie Jagd im urbanen Raum von Berlin. *Senatsverwaltung fuer Stadt und Umwelt, Berliner Forsten*.
- Hsu, M.J., Kao, C.C. & Agoramorthy, G. (2009) Interactions between Visitors and Formosan Macaques (*Macaca cyclopis*) at Shou-Shan Nature Park, Taiwan. *American Journal of Primatology*, **71**, 214-222.
- Hughes, J. & Macdonald, D.W. (2013) A review of the interactions between free-roaming domestic dogs and wildlife. *Biological Conservation*, **157**, 341-351.
- Janeau, G., Cousse, S., Cargnelutti, B. & Spitz, F. (1995) Role of daily movements in the sociospatial organization of wild boar populations (*Sus-scrofa* L). *Revue D Ecologie-La Terre Et La Vie*, **50**, 35-48.

- Jansen, A., Luge, E., Guerra, B., Wittschen, P., Gruber, A.D., Loddenkemper, C., Schneider, T., Lierz, M., Ehlert, D., Appel, B., Stark, K. & Noeckler, K. (2007) Leptospirosis in urban wild boars, Berlin, Germany. *Emerging Infectious Diseases*, **13**, 739-742.
- Jarolimek, J., Vanek, J., Jezek, M., Masner, J. & Stoces, M. (2014) The telemetric tracking of wild boar as a tool for field crops damage limitation. *Plant Soil and Environment*, **60**, 418-425.
- Jayakody, S., Sibbald, A.M., Gordon, I.J. & Lambin, X. (2008) Red deer *Cervus elephus* vigilance behaviour differs with habitat and type of human disturbance. *Wildlife Biology*, **14**, 81-91.
- Johnson, D.H. (1980) The comparison of usage and availability measurements for evaluating resource preference. *Ecology*, **61**, 65-71.
- Keuling, O., Stier, N. & Roth, M. (2008) Annual and seasonal space use of different age classes of female wild boar *Sus scrofa* L. *European Journal of Wildlife Research*, **54**, 403-412.
- Keuling, O., Stier, N. & Roth, M. (2009) Commuting, shifting or remaining? Different spatial utilisation patterns of wild boar *Sus scrofa* L. in forest and field crops during summer. *Mammalian Biology*, **74**, 145-152.
- Keuling, O., Strauss, E. & Siebert, U. (2016) Regulating wild boar populations is "somebody else's problem"! - Human dimension in wild boar management. *Science of the Total Environment*, **554**, 311-319.
- Kopetzki, S. (2016) personal communication with the hunting consultant of Berlin about wild boar hunting strategies in Berlin.
- Kotulski, Y. & König, A. (2008) Conflicts, crises and challenges: wild boar in the Berlin City—a social empirical and statistical survey. *Natura Croatica*, **17**, 233-246.
- Krebs, J.R. (1978) Optimal foraging: decision rules for predators. *Behavioural ecology: An evolutionary approach*, 23-63.
- Laundre J. W., Hernandez L. & Ripple W. J. (2010) The Landscape of Fear: Ecological Implications of Being Afraid. *The Open Ecological Journal*, **3**, 1-7.
- Laundre, J.W., Hernandez, L., Lopez Medina, P., Campanella, A., Lopez-Portillo, J., Gonzalez-Romero, A., Grajales-Tam, K.M., Burke, A.M., Gronemeyer, P. & Browning, D.M. (2014) The landscape of fear: the missing link to understand top-down and bottom-up controls of prey abundance? *Ecology*, **95**, 1141-1152.
- Laznik, Z. & Trdan, S. (2014) Evaluation of different soil parameters and wild boar (*Sus scrofa* L.) grassland damage. *Italian Journal of Animal Science*, **13** (4), 3434.
- Lewis, D.L., Baruch-Mordo, S., Wilson, K.R., Breck, S.W., Mao, J.S. & Broderick, J. (2015) Foraging ecology of black bears in urban environments: guidance for human-bear conflict mitigation. *Ecosphere*, **6**, 1-18.
- Lima, S.L. (1998) Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. *Advances in the Study of Behavior*, **27**, 215-290.
- Lima, S.L. & Dill, L.M. (1990) Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, **68**, 619-640.
- Lowry, H., Lill, A. & Wong, B.B.M. (2013) Behavioural responses of wildlife to urban environments. *Biological Reviews*, **88**, 537-549.
- MacArthur, R.H. & Pianka, E.R. (1966) On optimal use of a patchy environment. *American Naturalist*, **100** (916) 603-609.
- Magle, S.B., Ruell, E.W., Antolin, M.F. & Crooks, K.R. (2010) Population genetic structure of black-tailed prairie dogs, a highly interactive species, in fragmented urban habitat. *Journal of Mammalogy*, **91**, 326-335.
- Maibeche, Y., Moali, A., Yahi, N. & Menard, N. (2015) Is Diet Flexibility an Adaptive Life Trait for Relictual and Peri-Urban Populations of the Endangered Primate *Macaca sylvanus*? *Plos One*, **10**, 22.
- Massei, G., Kindberg, J., Licoppe, A., Gacic, D., Sprem, N., Kamler, J., Baubet, E., Hohmann, U., Monaco, A., Ozolins, J., Cellina, S., Podgorski, T., Fonseca, C., Markov, N., Pokorny, B., Rosell, C. & Nahlik, A. (2015) Wild boar populations up, numbers of hunters down? A review of trends and implications for Europe. *Pest Management Science*, **71**, 492-500.

- McKinney, M.L. (2002) Urbanization, biodiversity, and conservation. *Bioscience*, **52**, 883-890.
- Merkle, J.A., Robinson, H.S., Krausman, P.R. & Alaback, P. (2013) Food availability and foraging near human developments by black bears. *Journal of Mammalogy*, **94**, 378-385.
- Morelle, K., Lehaire, F. & Lejeune, P. (2014) Is wild boar heading towards movement ecology? A review of trends and gaps. *Wildlife Biology*, **20**, 196-205.
- Morelle, K., Podgorski, T., Prevot, C., Keuling, O., Lehaire, F. & Lejeune, P. (2015) Towards understanding wild boar *Sus scrofa* movement: a synthetic movement ecology approach. *Mammal Review*, **45**, 15-29.
- Murray, M., Cembrowski, A., Latham, A.D.M., Lukasik, V.M., Pruss, S. & St Clair, C.C. (2015) Greater consumption of protein-poor anthropogenic food by urban relative to rural coyotes increases diet breadth and potential for human-wildlife conflict. *Ecography*, **38**, 1235-1242.
- Murray, M.H. & St Clair, C.C. (2015) Individual flexibility in nocturnal activity reduces risk of road mortality for an urban carnivore. *Behavioral Ecology*, **26**, 1520-1527.
- Nasiadka, P. & Janiszewski, P. (2015) Food preferences of wild boars (*Sus scrofa* L.) in the summer and early autumn expressed by the damage caused in agricultural crops. *Sylvan*, **159**, 307-317.
- Naughton-Treves, L., Treves, A., Chapman, C. & Wrangham, R. (1998) Temporal patterns of crop-raiding by primates: linking food availability in croplands and adjacent forest. *Journal of Applied Ecology*, **35**, 596-606.
- Naves, J., Wiegand, T., Revilla, E. & Delibes, M. (2003) Endangered species constrained by natural and human factors: The case of brown bears in northern Spain. *Conservation Biology*, **17**, 1276-1289.
- Nowak, D.J., Noble, M.H., Sisinni, S.M. & Dwyer, J.F. (2001) People and trees: assessing the US urban forest resource. *Journal of Forestry*, **99**, 37-42.
- Ohashi, H., Saito, M., Horie, R., Tsunoda, H., Noba, H., Ishii, H., Kuwabara, T., Hiroshige, Y., Koike, S. & Hoshino, Y. (2013) Differences in the activity pattern of the wild boar *Sus scrofa* related to human disturbance. *European Journal of Wildlife Research*, **59**, 167-177.
- Otoni, I., de Oliveira, F.F.R. & Young, R.J. (2009) Estimating the diet of urban birds: The problems of anthropogenic food and food digestibility. *Applied Animal Behaviour Science*, **117**, 42-46.
- Pauleit, S., Jones, N., Garcia-Martin, G., Garcia-Valdecantos, J.L., Rivière, L.M., Vidal-Beaudet, L., Bodson, M. & Randrup, T.B. (2002) Tree establishment practice in towns and cities—Results from a European survey. *Urban Forestry & Urban Greening*, **1**, 83-96.
- Pierce, G.J. & Ollason, J.G. (1987) 8 reasons why optimal foraging theory is a complete waste of time. *Oikos*, **49**, 111-118.
- Podgorski, T., Bas, G., Jedrzejewska, B., Soennichsen, L., Sniezko, S., Jedrzejewski, W. & Okarma, H. (2013) Spatiotemporal behavioral plasticity of wild boar (*Sus scrofa*) under contrasting conditions of human pressure: primeval forest and metropolitan area. *Journal of Mammalogy*, **94**, 109-119.
- Pulliam, H.R. (1988) Sources, sinks, and population regulation. *American Naturalist*, **132**, 652-661.
- Pyke, G.H. (1984) Optimal foraging theory: a critical review. *Annual review of ecology and systematics*, **15**, 523-575.
- Pyke, G.H., Pulliam, H.R. & Charnov, E.L. (1977) Optimal foraging: a selective review of theory and tests. *Quarterly Review of Biology*, **52**, 137-154.
- Rosner, S., Mussard-Forster, E., Lorenc, T. & Muller, J. (2014) Recreation shapes a "landscape of fear" for a threatened forest bird species in Central Europe. *Landscape Ecology*, **29**, 55-66.
- Sáez-Royuela, C. & Telleria, J. (1986) The increased population of the wild boar (*Sus scrofa* L.) in Europe. *Mammal Review*, **16**, 97-101.
- Schley, L. & Roper, T.J. (2003) Diet of wild boar *Sus scrofa* in Western Europe, with particular reference to consumption of agricultural crops. *Mammal Review*, **33**, 43-56.
- Schmidt, K. & Kuijper, D.P.J. (2015) A "death trap" in the landscape of fear. *Mammal Research*, **60**, 275-284.

- Servanty, S., Gaillard, J.-M., Toigo, C., Brandt, S. & Baubet, E. (2009) Pulsed resources and climate-induced variation in the reproductive traits of wild boar under high hunting pressure. *Journal of Animal Ecology*, **78**, 1278-1290.
- Seto, K.C., Fragkias, M., Guneralp, B. & Reilly, M.K. (2011) A Meta-Analysis of Global Urban Land Expansion. *Plos One*, **6**, 9.
- Sönnichsen, L., Bokje, M., Marchal, J., Hofer, H., Jędrzejewska, B., Kramer-Schadt, S. & Ortmann, S. (2013) Behavioural responses of European roe deer to temporal variation in predation risk. *Ethology*, **119**, 233-243.
- Stillfried, M., Belant, J.L., Svoboda, N.J., Beyer, D.E. & Kramer-Schadt, S. (2015) When top predators become prey: black bears alter movement behaviour in response to hunting pressure. *Behavioural Processes*, **120**, 30-39.
- Stoen, O.G., Ordiz, A., Evans, A.L., Laske, T.G., Kindberg, J., Frobert, O., Swenson, J.E. & Arnemo, J.M. (2015) Physiological evidence for a human-induced landscape of fear in brown bears (*Ursus arctos*). *Physiology & Behavior*, **152**, 244-248.
- Theimer, T.C., Clayton, A.C., Martinez, A., Peterson, D.L. & Bergman, D.L. (2015) Visitation rate and behavior of urban mesocarnivores differs in the presence of two common anthropogenic food sources. *Urban Ecosystems*, **18**, 895-906.
- Thurfjell, H., Spong, G. & Ericsson, G. (2013) Effects of hunting on wild boar *Sus scrofa* behaviour. *Wildlife Biology*, **19**, 87-93.
- Tigas, L.A., Van Vuren, D.H. & Sauvajot, R.M. (2002) Behavioral responses of bobcats and coyotes to habitat fragmentation and corridors in an urban environment. *Biological Conservation*, **108**, 299-306.
- Tryjanowski, P., Skorka, P., Sparks, T.H., Biadun, W., Brauze, T., Hetmanski, T., Martyka, R., Indykiewicz, P., Myczko, L., Kunysz, P., Kawa, P., Czyz, S., Czechowski, P., Polakowski, M., Zduniak, P., Jerzak, L., Janiszewski, T., Golawski, A., Dudus, L., Nowakowski, J.J., Wuczynski, A. & Wysocki, D. (2015) Urban and rural habitats differ in number and type of bird feeders and in bird species consuming supplementary food. *Environmental Science and Pollution Research*, **22**, 15097-15103.
- Walther, F.R. (1969) Flight behaviour and avoidance of predators in Thomson's gazelle (*Gazella thomsoni* Guenther 1884). *Behaviour*, **34**, 184-220.
- Wandeler, P., Funk, S.M., Lurgiader, C.R., Gloor, S. & Breitenmoser, U. (2003) The city-fox phenomenon: genetic consequences of a recent colonization of urban habitat. *Molecular Ecology*, **12**, 647-656.

CHAPTER 2: Manuscript 1

Wild Boar Population Genetics

Do cities represent sources, sinks or isolated islands for urban wild boar population structure?

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Author contribution:

Conceptual framework and predictions of this study were discussed and developed by Milena Stillfried (MS), Alain Frantz (AF), Stephanie Kramer-Schadt (SKS) and Sylvia Ortmann (SO). A majority of the samples were collected by MS and Konstantin Börner (KB); the remaining samples were collected by Ulrich Wittstatt (UW) and Mike Heddergott (MH). Laboratory analyses were conducted by AF and by Tanja Noventa under supervision of Jörns Fickel (JF). The statistical analyses were conducted by MS and AF. The manuscript was written by MS, extensively commented on and edited by AF and also edited by JF, SKS and SO.

Do cities represent sources, sinks or isolated islands for urban wild boar population structure?

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Summary

1. Urban sprawl has resulted in the permanent presence of large mammal species in urban areas, leading to human–wildlife conflicts. Wild boar (*Sus scrofa*) are establishing a permanent presence in many cities in Europe, with the largest German urban population occurring in Berlin. Despite their relatively long-term presence there is little knowledge of colonisation processes, dispersal patterns or connectivity of Berlin’s populations, hampering the development of effective management plans.

2. We used 13 microsatellite loci to genotype 387 adult and sub-adult wild boar from four urban forests, adjacent built-up areas and the surrounding rural forests. We applied genetic clustering algorithms to analyse the population genetic structure of the urban boar. We used Approximate Bayesian Computation to infer the boar’s colonisation history of the city. Finally, we used assignment tests to determine the origin of wild boar hunted in the urban built-up areas.

3. The animals in three urban forests formed distinct genetic clusters, with the remaining samples all being assigned to one rural population. One urban cluster was founded by individuals from another urban cluster rather than by rural immigrants.

4. The wild boar that had been harvested within urban built-up areas were predominantly assigned to the rural cluster surrounding the urban area, rather than to one of the urban clusters.

5. *Synthesis and applications.* Our results are likely to have an immediate impact on management strategies for urban wild boar populations in Berlin, because they show that there are not only distinct urban clusters, but also on-going source–sink dynamics between urban and rural areas. It is therefore essential, that the neighbouring Federal States of Berlin and Brandenburg develop common hunting plans to control the wild boar population and reduce conflicts in urban areas.

Key-words: urban ecology, urban-rural-gradient, movement barrier, human-wildlife-conflict, DIYABC, STRUCTURE, BAPS, microsatellites, Berlin, hunting, source–sink dynamics

For copyright reasons, the article is not included in the online version of this thesis. An electronic version of the article is available at:

<http://dx.doi.org/10.1111/1365-2664.12756>

CHAPTER 3: Manuscript 2

Wild Boar Habitat Use

Secrets of success in a landscape of fear: Urban wild boar use habitats that rural conspecifics avoid

(in prep.)

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Author contribution:

Conceptual framework and predictions of this study were discussed and developed by Milena Stillfried (MS), Stephanie Kramer-Schadt (SKS) and Sylvia Ortmann (SO).

MS and Konstantin Börner (KB) caught wild boar and collected data; Frank Göritz (FG), Johanna Painer (JP) and Kathleen Röllig (KR) performed wild boar anaesthesia; Moritz Wenzler (MW) created spatial land cover maps; MS, Heribert Hofer (HH) and SKS performed the statistical analysis; The manuscript was written by MS, extensively commented on and edited by SKS, SO and HH.

All authors read and commented on the manuscript.

Secrets of success in a landscape of fear: Urban wild boar use habitats that rural conspecifics avoid

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Summary

Wild boar (WB, *Sus scrofa*) is an excellent model to analyse how the landscape of fear, an individual's perception of risk, may be adjusted to the specific conditions of rural and urban environments when trading-off access to food. With the help of GPS collars with high spatial and temporal resolution, space use, movements and activity patterns of 11 WB from the region in and around the urban areas of Germany's capital Berlin were analysed on two hierarchical levels of habitat selection: How do size and location of home ranges depend on landscape variables related to food or fear, and how does habitat use within home ranges relate to movement patterns and the characteristics and use of WB resting sites and sites of activity? When housing and human population density was high, urban WB had smaller home ranges and more suitable resting sites than rural WB. By choosing areas close to roads as resting sites and foraging close to housing, urban WB adjusted their perception of risk while rural WB avoided these areas. WB therefore showed considerable behavioural plasticity suitable to adjust to human-dominated environments in a potentially evolutionarily adaptive manner.

Key-words: behavioural adjustment, GPS-telemetry, habitat selection, human wildlife conflict, ungulate, urban ecology, wildlife, mammal, correlated random walk, movement algorithm

Introduction

The 'landscape of fear' model describes an animal's trade-off between access to food and predator avoidance on a spatial scale (Brown, Laundre & Gurung 1999; Laundre J. W., Hernandez L. & Ripple W. J. 2010; Laundre *et al.* 2014). Disturbance of wildlife by people is particularly frequent in urban environments and can exceed disturbance by natural predators. It therefore has the potential to shape prey behaviour and should incite avoidance of such environments (Frid & Dill 2002; Ciuti *et al.* 2012; Rosner *et al.* 2014; Stoen *et al.* 2015). Nevertheless, the number of mammal species which inhabit human dominated landscapes and enter and live in urban environments is on the increase (Bateman & Fleming 2012; Magle *et al.* 2012). On the one hand, urban environments provide a diverse and potentially attractive foraging landscape, which contains anthropogenic, easily accessible food sources (Cahill *et al.* 2012; Murray *et al.* 2015; Theimer *et al.* 2015; Tryjanowski *et al.* 2015) with a high amount of energy (Ottoni, de Oliveira & Young 2009; Maibeche *et al.* 2015). On the other hand, the landscape of fear in urban environments should be worse than in rural environments because the sources of danger are increased in frequency and intensity because of human proximity *per se*, a high traffic volume and additional predators such as pets (domestic dogs and other companion animals, Frid & Dill 2002; Baker *et al.* 2005; Hughes & Macdonald 2013). In order to successfully operate in such a landscape with an apparent increase in danger levels, urban wildlife must be aware of such changes in the landscape of fear and have the ability to adjust to it in order to secure sufficient shelter, breeding sites and food (McKinney 2002; Lowry, Lill & Wong 2013). Wildlife with sufficient cognitive abilities would need to perceive spatial variation in danger levels and should be able to imagine spatial layers of the environment where each layer is directly related to a landscape factor (Valeix *et al.* 2012). In urban wildlife, the layer of the landscape of fear is likely to consist of key landscape feature such as roads, because of vehicle and pedestrian traffic (Dowding *et al.* 2010; Bonnot *et al.* 2013; Lowry, Lill & Wong 2013; Morelle, Lehaire & Lejeune 2013; Murray & St Clair 2015; Thurffjell *et al.* 2015; Gray *et al.* 2016), and sealed built-up areas with a high density of housing (Bonnot *et al.* 2013; Magle *et al.* 2014; Beninde, Veith & Hochkirch 2015; Gray *et al.* 2016) without cover but high human activity and population density. Resource hotspots for food and shelter may often be found in more natural habitats

such as forests, parks, water bodies or swamp areas close to water (Beninde, Veith & Hochkirch 2015; Morelle *et al.* 2015).

Modulation of behaviour, particularly space use, can be tested at different levels of habitat selection (Johnson 1980). At the level of the entire home range (second order of habitat selection, Johnson 1980), urban foxes (*Vulpes vulpes*) in Oxford, for example, responded to the instability of the urban landscape of fear by drifting territories (Doncaster & Macdonald 1991), whereas in Bristol they had a high degree of spatiotemporal stability in their home ranges (White, Saunders & Harris 1996). Similarly, home range sizes of urban coyotes (*Canis latrans*) showed a high seasonal variability in some but not all cities (Grinder & Krausman 2001). Home ranges of bobcats (*Lynx rufus*) and coyotes in Los Angeles were of a similar size in fragmented urban and in rural areas, probably because the size of inaccessible built-up areas within a home range may have been balanced by the easy availability of anthropogenic food (Tigas, Van Vuren & Sauvajot 2002).

In order to identify the behavioural choices of urban wildlife and their ability to perceive and respond to spatial and temporal variation in risk as well as food availability, the actual resource use within specific habitat components of the home range (third order of habitat selection, Johnson 1980) is the appropriate scale for studying potential behavioural adjustments. For instance, at this scale it was demonstrated that urban hedgehogs avoided foraging close to roads but could not avoid having to cross roads (Dowding *et al.* 2010). Urban bobcats and coyotes coped with habitat fragmentation and the presence of people in urban environments by avoiding encounters, because they were willing to cross roads (Tigas, Van Vuren & Sauvajot 2002). Urban coyotes adjusted the timing of road crossings in relation to human activity to reduce the risk of vehicle collision (Murray & St Clair 2015), which demonstrated an understanding of spatial and temporal variation of risk within their urban environment. Another example for a behavioural adjustment to urban environments are animals which find and use green patches (Beninde, Veith & Hochkirch 2015) and areas with a high vegetation density (as measured by NDVI (normalized differenced vegetation index), Bino *et al.* 2008) in order to maintain space use and movements at a rate similar to rural environments, as observed for urban cougars (*Puma concolor*, Kertson *et al.* 2011).

Studies on urban mammals are often conducted with medium-sized mammals such as foxes, badgers or coyotes (Gloor *et al.* 2001; Grinder & Krausman 2001; Davison *et al.* 2008; Gehrt, Anchor & White 2009) but studies on large social mammals in urban areas are rare. Wild boars (*Sus scrofa*, abbreviated as WB) are social mammals with a growing population

throughout Europe (Massei *et al.* 2015; Keuling, Strauss & Siebert 2016) and an increased presence in urban areas (Dinter 1991; Cahill, Llimona & Gracia 2003; Jansen *et al.* 2007; Cahill *et al.* 2012; Podgorski *et al.* 2013). WBs are frequently in conflict with people because they are potential transmitters of zoonotic diseases or diseases relevant to livestock (Fernández, Kramer-Schadt & Thulke 2006; Jansen *et al.* 2007; Chiari *et al.* 2015) and because they can destroy agricultural crops and therefore could be responsible for economic damage (Amici *et al.* 2012; Ficetola *et al.* 2014; Jarolimek *et al.* 2014; Laznik & Trdan 2014). They are therefore a most useful model species to study the ability of wildlife to perceive and respond to spatial variation in the landscape of fear and the distribution of resources, thereby assisting local authorities to develop appropriate management tools to minimise potential wildlife-human conflict. Despite numerous studies on WB which demonstrated substantial variation in home range size and kinetics of movements in natural and agricultural landscapes (Dardaillon & Beugnon 1987; Cousse *et al.* 1992; Janeau *et al.* 1995; Thurfjell, Spong & Ericsson 2013; Jarolimek *et al.* 2014; Morelle, Lehaire & Lejeune 2014; Morelle *et al.* 2015), studies about urban WB are rare (Cahill, Llimona & Gracia 2003; Cahill *et al.* 2012; Podgorski *et al.* 2013).

In this study, we collected and analysed GPS data of WB for the first time along an urban-rural gradient, investigating the home ranges and movements of WB in urban areas of Germany's capital Berlin in comparison with neighbouring rural areas. We analysed space use as movements within a landscape of fear where we investigated its spatial variation at different scales – the home range level (second order of habitat selection) and the fine scaled space use within the home range (third order of habitat selection). For both analyses, we designed a set of candidate models to identify the WB's perception of the landscape of fear and its spatial variation and the distribution of food through the movement choices of WB. For the analysis of the size and dynamic shift of home ranges and dynamic shifts in resting sites, we used the relative proportion of habitat variables that made up a home range as proxies for either the landscape of fear or the landscape of food. For the third order analysis of habitat selection and habitat use within the home range, we used various distances to landscape features as proxies for the landscape of food and fear.

We hypothesised that WB in urban environments adjusted their perception of risk, i.e. modulated their landscape of fear, in order to find sufficient food and shelter in a novel environment. Further, we hypothesised that the trade-off between fear and food will be biased in favour of food, if the potential rewards in the urban environment are higher than in the rural

one, and therefore that the modulation of the landscape of fear is stronger than the modulation of the landscape of food. We therefore predicted that

- (1) urban WB have smaller home ranges due to a rich diet but that they have to shift their home range more often than rural WB as a response to the human-induced landscape of fear;
- (2) within the home range, urban WB have to adjust to the landscape of fear on a spatial scale by selecting landscape elements with a decreased or predictable disturbance;
- (3) in order to avoid humans, urban WB have to adjust to human activity and modulate their behaviour not only on a spatial but also on temporal (daily and seasonal) scale.

Materials and methods

STUDY AREA

The study was carried out in the city state of Berlin (52°31'N, 13°24'E) and adjoining parts of the Federal State of Brandenburg, Germany (Fig. 3.1). Twenty percent of the area of Berlin is covered with urban forests which are divided into four management units, of which the Grunewald (southwest) and Pankow (north) areas were used for the study. The Grunewald is a mixed forest with a substantial number of human visitors (1 million visits annually, BDF 2015; Franusch 2015) west of the neighbouring urban built-up areas. Although more than 1000 WB are hunted every year in the Grunewald alone (Stillfried et al. 2016), the number of WB remains high, and they can be regularly observed in urban forests and built-up areas even during the day. The Grunewald is bordered by rural coniferous forests (Potsdam area, Fig. 3.1) in the west, which were also included in the study. The Pankow area is less forested and is also located next to urban built-up areas, for example Glienicke Nordbahn where WB groups are regularly observed, even during the day. A third component of the study area were the urban and rural areas in Strausberg, a small city to the east of Berlin. WB are common in the urban forests of Berlin and have been hunted here since World War II (Dinter 1991; Hespeler 2007). To reduce human-wildlife conflicts, hunting within built-up areas of Berlin was established in 2000 owing to the increased presence of WB within built-up areas of Berlin, creating a permanent hunting pressure (Hespeler 2007).

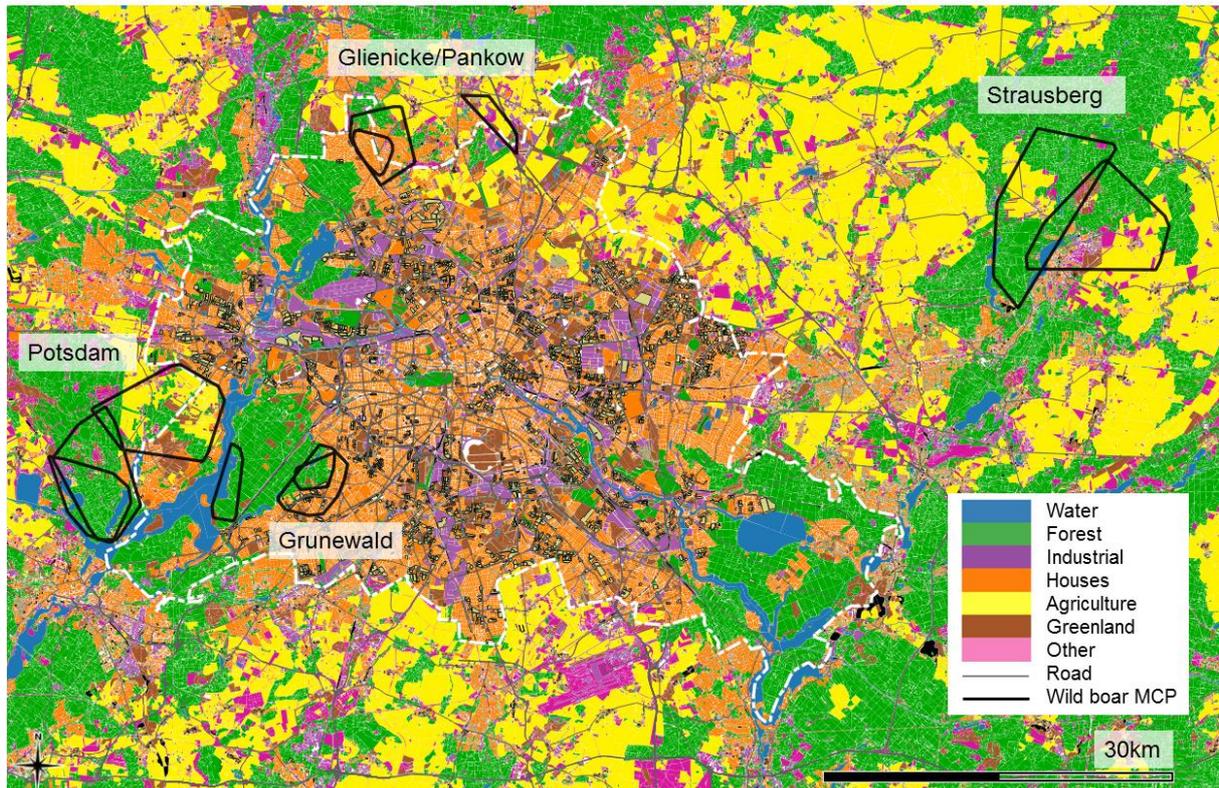


Fig. 3.1: Distribution of main habitat categories and wild boar trapping locations across the study area in Berlin and Brandenburg. Thirteen wild boar were caught and named according to the order of the capture date, but since two dropped their collars after two weeks, only 11 individuals were included in the analysis: Three individuals (IZW1, IZW5, IZW9) were collared in the Grunewald, three (IZW2, IZW6, IZW12) were collared in the Potsdam area, three (IZW3, IZW4, IZW13) were collared in Glienicke/Pankow and two (IZW7, IZW8) in the Strausberg area. The main habitat categories were water bodies, forest, industrial areas, housing, agriculture and open green space and are displayed in different colours. The black lines show 100 % minimum convex polygons of home ranges of radio-collared wild boar included in the study. The map was created with QGIS version 2.14.1 (QGIS-Development-Team, Essen, Germany, <http://qgis.org/downloads/>).

ANIMAL CAPTURE, HANDLING AND DATA COLLECTION

WB were caught in collaboration with Berlin's and Brandenburg's foresters between 2013 and 2015 using two by two meter iron traps developed by Hinrich Zoller (University of Rostock, Germany). Owing to the high activity of people or domestic dogs in urban forests, even at night, traps in Berlin were manually activated using a live video observation system, also developed by Hinrich Zoller (University of Rostock, Germany). Trapping was conducted by a team of researchers and foresters. Traps in Brandenburg were set to be automatically activated. Traps were equipped with trap transmitters (Vectronic Aerospace, Berlin Germany) which send a message when the trap had been triggered and with camera traps (Seissiger, Würzburg, Germany), which send live pictures via email to actually see the trapped animal. The trapping mechanism was triggered by a horizontally strained wire, which ensured that

piglets and small animals could enter the trap and walk below the wire without triggering the trap. No other animals than adult WB were caught. Owing to the described observation systems, time between capture and handling did not exceed three hours. Animals were immobilized using a remote dart system, equipped with 3 cc darts (Daninject, Børkop, Denmark) and a dart-pistol (Daninject, Børkop, Denmark) set to 2.5 bar for short distances in the trap. For anaesthesia, we applied the permitted combination of 8.0 mg/kg of 10 % ketamine (Bremer Pharma, Warburg, Germany) and 10.0 mg/kg Xylazine (Rompun™, Bayer, Leverkusen, Germany) which is judged to be suitable for wildlife which may be hunted for potential human consumption. Throughout anaesthesia, individuals were supplemented with nasal oxygen. Eye ointment was provided and eyes were covered for protection. Intravenous isotonic infusion (0.9 % NaCl, Braun, Melsungen, Germany) was applied to hyperthermic individuals. The animals were monitored during anaesthesia for body temperature, pulse, respiration and oxygen saturation by pulseoxymetry, they were weighed and sexed, and their health status was assessed by external examination. We attached global positioning system collars (GPS Pro Light Collar, Vectronic Aerospace, Berlin, Germany; approximate weight 1300g, equivalent to < 2 % of body weight) programmed to obtain a location every 30 minutes and ear tags to identify study animals after releasing the collar. If piglets were caught together with their mother, they were also equipped with ear tags. Each WB was released at its respective capture location. GPS locations were automatically transferred via GSM (Global System for Mobile Communication) and downloaded with the software GPSPlusX (Vectronic Aerospace, Berlin, Germany). We hereby confirm that animal handling permits were issued by the respective animal welfare licensing committee of Berlin (“Landesamt für Gesundheit und Soziales“/ LaGeSo: permit number: Reg 0383/12) and Brandenburg (“Landesamt für Umwelt, Gesundheit und Verbraucherschutz“: permit number: V3-2347-40-2012). All methods used were in accordance with these permits and the ASAB/ABS Guidelines for the Use of Animals in Research.

HABITAT CLASSIFICATION AND EXPLANATORY VARIABLES

A geographic database for Berlin and Brandenburg was established in order to provide spatial information that can be used for analyses of urban mammals in Berlin and Brandenburg. The database contained up-to-date biological habitat maps for Berlin from 2010, downloaded with

Tab. 3.1: Definition and use of habitat categories and other factors which may influence space use by wild boars within the conceptual framework of the study.

Name	Variable description	Related study	Expected influence
Season	Winter versus summer	Wild boar (Calenge <i>et al.</i> 2002; Keuling, Stier & Roth 2008; Thurfjell, Spong & Ericsson 2013; Thurfjell, Spong & Ericsson 2014)	variation of food + fear variables
Origin	Rural versus urban	Wild boar (Cahill, Llimona & Gracia 2003; Cahill <i>et al.</i> 2012; Podgorski <i>et al.</i> 2013)	
2nd order analysis of habitat use: proportions of various habitats			
%Forest	Percentage of forest (deciduous and coniferous) in monthly home range (mHR)	Review species richness (Beninde, Veith & Hochkirch 2015), Review WB movement (Morelle <i>et al.</i> 2015)	food
%Water	Percentage of water (water bodies, shorelines, swamp) in mHR	Review species richness (Beninde, Veith & Hochkirch 2015), Review WB movement (Morelle <i>et al.</i> 2015)	food
%Houses	Percentage of houses (house with garden, public and private buildings) in mHR	puma (Gray <i>et al.</i> 2016), urban coyote and deer (Magle <i>et al.</i> 2014), Review species richness (Beninde, Veith & Hochkirch 2015)	fear
cross	number of road crossing events (major roads and motorways) in mHR	urban coyote (Murray & St Clair 2015), WB (Morelle, Lehaire & Lejeune 2013; Thurfjell <i>et al.</i> 2015), Review urban wildlife (Lowry, Lill & Wong 2013)	fear
3rd order analysis of habitat use: distances to key habitat features within the home range			
D_Forest	Distance of WB location (WBL) to forest (deciduous and coniferous)	Review species richness (Beninde, Veith & Hochkirch 2015), Review WB movement(Morelle <i>et al.</i> 2015)	food
NDVI	Normalized density vegetation index at WBL	urban birds (Bino <i>et al.</i> 2008), ungulates (Borowik <i>et al.</i> 2013)	food
D_Water	Distance of WBL to water (water bodies and shorelines with swamp)	Review species richness (Beninde, Veith & Hochkirch 2015), Review WB movement (Morelle <i>et al.</i> 2015)	food
D_Houses	Distance of WBL to houses (house with gardens, public and private buildings)	roe deer (Bonnot <i>et al.</i> 2013)	fear
D_Roads	Distance WBL to roads (only major roads and motorways)	urban wildlife (Lowry, Lill & Wong 2013), urban hedgehog (Dowding <i>et al.</i> 2010), puma (Gray <i>et al.</i> 2016), roe deer (Bonnot <i>et al.</i> 2013), WB (Morelle, Lehaire & Lejeune 2013)	fear

permission from the “Senatsverwaltung für Stadt und Umwelt” (fisbroker.de), and Brandenburg, downloaded with permission from the website of the Ministry of Rural Development, Environment and Agriculture of the Federal State of Brandenburg (MRDEA, biotop and landuse mapping in Brandenburg, CIR-biotop types 2009), and were merged using ESRI ArcGIS 10.0 (ESRI Inc., Redlands, CA, USA). Since both source maps contained 1,351 habitat categories which were not identical, we reclassified land cover into main habitat categories which the literature suggested would be of interest to understand WB space use. We did this as follows: We separated the classes into food variables (mixed forest and coniferous forest, agriculture, water shorelines and swamp) and categories creating a potential landscape of fear because of a lack of shelter or human presence (fallow land, industrial, houses with gardens, private and public buildings, private and public green spaces, roads and railways, Fig. 3.1). As an additional variable for food availability, we downloaded with permission normalized difference vegetation index maps (NDVI) created by Landsat (<http://earthexplorer.usgs.gov/>, downloaded on September 16, 2015), using pictures from March, April, June, August and November, each with a resolution of 30 x 30 m. After consulting the relevant literature (Tab. 3.1) and considering the actual presence of habitats (Fig. 3.1), we selected only the most important habitats as proxies for the landscape of food and fear (Tab. 3.1) variables.

DATA ANALYSIS

All WB were grouped into urban and rural individuals with the help of trapping location, distance to the geographical centre of the city state of Berlin, number of visitors and human population density present within the home range (Fig. 3.2). The trapping location was either in human dominated landscapes such as settlements, domestic dog exercising areas, close to motorways, or in rural forests. The distance of each home range to the geographical centre of the city state of Berlin was measured in km, distances below 15km were marked as urban, distances above 15km were mostly outside the city state of Berlin and therefore used as indicator to classify a WB as rural. The annual number of visitors was estimated with the help of camera traps at the trapping locations and marked as either low or very high (locations where visitor numbers exceeded those of areas with low numbers by at least two orders of magnitude). For human population density within the home range of each individual, we used reported densities for the respective administrative districts (source: [57](https://www.statistik-</p></div><div data-bbox=)

berlin-brandenburg.de/, Fig. 3.2). WB with three urban categories were assigned to belong to the urban group, all others were classified as rural.

The flight distance from people was recorded for each individual during field observations. Each animal was observed for a minimum of five times. The distance was estimated in 5m steps when WB could be observed. For WB which could not be visually observed, we estimated the flight distance to be a minimum of 100 m, using the strength of the VHF signal of the GPS collar as an indicator that the animal moved away when we came closer to resting sites. Actual distances might have well exceeded 100 m. To test the difference between the urban and rural group, we used a Wilcoxon-Mann-Whitney test on the ranks of flight distances. The mean flight distances and their 95 % confidence interval, were calculated with the exact and minimum (censored) estimates for both urban and rural WB with a Kaplan-Meier survival analysis in Systat version 13 (Systat Software Inc., Richmond, VA, USA).

The GPS locations recorded from all WB were merged into a single dataset containing 78,293 locations, and used to calculate the nearest distance to water, housing, forests and roads using the QGIS (version 2.14.1, QGIS-Development-Team, Essen, Germany) extension NNjoin Plugin (version 1.2.2.). We additionally intersected all locations with the five seasonal NDVI maps. Distances and NDVI values were added to the dataset. We then calculated home ranges (and their size) using the 100% minimum convex polygon method (mcp), 95% mcp and 95% kernel utilisation density in R (version 3.2.2., R Core Development Team 2015), using the package `adehabitatHR` version 0.4.14 (Calenge 2006) for every WB for each observed month. Resting sites were identified by extracting locations which were collected during inactive hours identified by visual inspection of actograms provided by bi-axial acceleration (ACC) sensors. The shift of the centroid of the home ranges and resting sites between different months was calculated as the net displacement between the two points. To investigate the frequency of road crossing events per month, WB trajectories were intersected with a polyline shapefile including only major roads and motorways, and each line intersection was counted as one road crossing event. We also calculated the percentage of forest, water bodies, housing for every monthly home range.

For the second order habitat selection analyses we ran linear mixed models (LMMs) and used values of home range size [100% mcp, 95% mcp and kernel utilisation density in km²], shift of home range centroids [m] and shift of resting sites [m] as response. Both food (percentage of forest and water bodies) and fear variables (percentage of housing, frequency of road

CHAPTER 3: Manuscript 2- Wild Boar Habitat Use

Wild boar ID, Sex, month/ year of collaring	Photographs of home ranges	Trapping location 	Dist. to centre 	Number of visitors 	Human population density 	Wild boar category (origin: urban or rural)
IZW13 , f 02/2015 - 04/2015		Glienicke NB, elementary school	14.6	very high	25-50	urban 
IZW4 , f 02/2014 - 10/2014		Glienicke NB, elementary school	14.9	very high	25-50	urban 
IZW9 , f 06/2014 - 12/2014		Grunewald dog exercising area	10.9	1 Mio = very high	25-50	urban 
IZW1 , f 07/2013 - 12/2013		Grunewald dog exercising area	10.3	1 Mio = very high	25-50	urban 
IZW5 , m 04/2014 - 10/2014		Grunewald, next to public bathing area	14.9	1 Mio = very high	25-50	urban 
IZW6 , m 05/2014 - 12/2014		Potsdam, forest / agricultural area	18.2	low	5-50	rural 
IZW3 , m 11/2013 - 03/2014		Pankow, next to motorway	14.3	low	5-50	rural 
IZW8 , f, 06/2014 - 12/2014		Strausberg, close to settlement	36.7	low	5-50	rural 
IZW2 , f, 07/2013 - 02/2014		Potsdam, forest	22.6	low	5-10	rural 
IZW12 , f, 08/2014 - 12/2014		Potsdam, forest	22.5	low	5-10	rural 
IZW7 , m 05/2014 - 03/2015		Strausberg, forest	34.1	low	> 5	rural 

Fig. 3.2: Classification of wild boar caught and collared between 2013 and 2015 in Berlin and Brandenburg. In total, thirteen wild boar were caught and named according to the order of the capture date, but since two dropped their collars after two weeks, only 11 individuals were included in the analysis. All female radio-collared individuals were lactating and members of social groups consisting of several females and young. Some of the young radio-collared males were in the company of other young males when we caught them but it is unknown how suitable these contacts were. *Photographs* give an impression of the particular home ranges of each wild boar and were taken during times when they were collared: (from top to bottom) (1) playground at the elementary school where IZW 13 and 4 were caught, (2) IZW4 and group at a house where they were fed, (3) rooting damage in a front garden after a visit of IZW9 and her group, (4) typical scenery from the domestic dog exercising areas where large groups of domestic dogs are taken for walks by special domestic dog walkers and wild boar observation at a main road in the Grunewald by our team (the wild boar is marked with a red arrow, because it is well camouflaged and difficult to see), (5) a member of our team receiving a VHF signal from IZW5 next to the bathing area whilst several people were swimming, (6) crop field damage found whilst tracking IZW6, (7) motorway next to the typical resting site and trapping location of IZW3, (8) IZW8 and her piglets before capture, (9) typical coniferous pine forests from the areas of IZW2, IZW12 and IZW7. *The distance to the centre* is the distance of the home range centroid of each wild boar to the geographical center of the city state of Berlin. *The number of visitors* was estimated as an annual number from official visitor numbers or was estimated from visitor occurrence around our trapping locations with help of camera traps. *Human population density* expresses the mean human population density per ha of the district with which the wild boar home range overlapped. Grey shading, if present, indicates high urban impact. Only wild boar with a minimum of three grey categories were assigned to the urban group. Photographs: M. Stillfried.

crossing events) were used as explanatory variables which were tested for interactions with season (summer, winter) and origin (rural, urban). For a detailed description of these variables see Tab. 3.1. The WB individual identifier and month were used as random effects to account for individual variation or seasonal effects. We compared a set of candidate models, including a full model with all variables, models including only food variables or only fear variables as well as a neutral model including only season and origin. An intercept model, containing only the random factors was also included in the set of candidate models to assess indifference of WB behaviour with respect to differences between habitats in the landscapes of food or fear. A list of all candidate models is provided in Tab. S 6.3.1. Candidate models were compared and ranked using Akaike's Information Criterion (Boyce et al. 2002) corrected for small sample size (AICc) and Akaike weights which provide conditional probabilities for each model and give insight into the relative merits of the competing models (Wagenmakers & Farrell 2004).

In order to test for habitat preferences in the third order habitat selection analyses, we compared the use of habitat variables by each individual with the availability of respective

habitat variables within reach of the animal (Manly et al. 2002; Boyce 2006; Johnson et al. 2006) as derived by simulated random movements. For a null model for spatially random movements which incorporated movement constraints we employed simulated correlated random walks (CRWs) parameterised on the basis of the WB movement data. CRWs use the step length and turning angle from the animal tracks and then simulate random trajectories within the study area based on these metrics. We used a buffered mcp yielding twice the size of the original mcp of each animal for each month and simulated five random walks per month per animal using the `adehabitatHR` R-package version 0.4.14 (Calenge 2006). Large water bodies were eliminated from the buffer to ensure that the simulated locations were not set within lakes, since lakes were bordering the home ranges of some individuals. The locations of the CRWs were then added to the WB data, resulting in a dataset with 469,758 locations. For each location we calculated the nearest distances to water bodies, roads, housing and forests using the QGIS tool `NNjoin` version 1.2.2 (Håvard Tveite, NMBU, Oslo, Norway) and added the habitat category for each location using QGIS `fTools Plugin` version 0.6.2 (Carson Farmer, Maynooth, Ireland). NDVI values for each location were added by using the value of the raster cell which overlapped with the GPS coordinate.

We visualized the distribution of urban and rural WB across habitats and simulated locations in different habitat classes using the R package `tableplot` version 0.3-5 (Tennekes 2016). Only the habitat classes that were most frequently used by WB were included in the further analyses. We also visualized the number of diurnally and nocturnally visited locations (day = inactive times for WB, starting at 7am and night = active times for WB, starting at 7pm) were identified by visual inspection of actograms provided by bi-axial acceleration (ACC) sensors) per habitat class.

We used the origin of WB (rural or urban) and season (summer or winter) as well as their interactions with the food variables (distances to water bodies and forests, NDVI values) and fear variables (distance to roads and housing) as explanatory variables in a binomial generalised linear mixed model (GLMM with logit link) with observed WB tracks (1) or CRW (0) as binary response variable and the individual identifier as random effect (Tab. 1). All explanatory variables were standardized using the function `'scale'` in R which calculates the mean and standard deviation (sd) of the entire vector, then "scales" each element by those values by subtracting the mean and dividing by the sd.

We chose a set of candidate models including an intercept only model, a neutral model without habitat variables and models containing only food or only fear variables and a full model (Tab. S 6.3.1). As described above, candidate models of the GLMMs were compared and ranked using AICc and model weight. A list of all candidate models can be found in Tab. S 6.3.1.

Prior to model fit, we first tested for potential correlations between predictor variables using correlation plots (Fig. S 6.3.2A). As GLMMs require a linear relationship between the transformed response in terms of the link function and the explanatory variables, we built binomial generalised additive models (GAMs (Hastie & Tibshirani 1987; Austin 2002; Wood 2004)) using WB movement data (1) and simulated movement (0) as response and fitted smoothing splines with 3 knots for the dependent variables distance to water bodies, forest, housing, roads and NDVI, using the R-package mgcv version 1.8-15. All variables were linear (guided by visual inspection of the partial residual plots together with GAM results, Fig. S 6.3.2, Klar et al. 2008)) so that no variable transformation was necessary for the final models. We repeated the whole procedure with GLMMs that used locations during the night (active times for WB = 1) and locations during the day (resting time for WB = 0) as response variables to distinguish between differences in temporal space use (list of candidate models in Tab. S 6.3.1). Model selection was based on AICc and AICc weights (Wagenmakers & Farrell 2004). We created effects plots and coefficient plots for all variables using the ‘effects’ version 3.1-1 and ‘sjPlot’ version 2.0.2 packages in R.

Results

We radio-tracked 13 radio-collared WB, nine females and four males, between 2013 and 2015. Since two females lost their collars after a few days, we only included seven females and four males in our analysis. Mean observation time was 6.0 ± 2 months, because four of our study animals were prematurely shot by hunters and two were killed by cars. For the surviving animals, we removed their collars using the drop-off transmitter function after six to eight months according to our animal handling permits. In total we collected 78,293 GPS locations.

Of all locations in urban areas 80.0 % ($n = 26,464$) were collected in habitat classes associated with the landscape of food and only 20.0 % ($n = 6,616$) in anthropogenic landscapes associated with the landscape of fear (Fig. S 6.3.1). With 95.0 % ($n = 42,951$), WB locations

in rural areas were almost exclusively located in the landscape of food. In comparison, when we simulated WB movement tracks using a correlated random walk algorithm, a higher percentage of fixes was located in the landscape of fear, with 35.0 % ($n = 75,891$) of simulated urban locations and 8.0 % ($n = 18,084$) of simulated rural locations in built up areas (Fig. S 6.3.1). During the day, 89 % ($n = 14,441$) of urban WB locations were located within the landscape of food and only 11 % ($n = 1,784$) in the landscape of fear. At night, 22 % ($n = 3,708$) of urban WB locations were collected in landscape of fear habitats (Fig. S 6.3.1).

FLIGHT DISTANCE

The flight distance of urban WB was significantly shorter than that of rural WB (Wilcoxon-Mann-Whitney U-test, $U = 1$, exact $p = 0.0065$, $n = 11$). The mean flight distance for urban WB was 31.0 m (95% CI 16.4 m – 45.5m, $n = 5$, Kaplan-Meier survivorship analysis), whereas the mean flight distance for rural WB was, at 92.5 m, almost three times higher (95% CI could not be computed because of censored data, $n = 6$, Fig. 3.3).

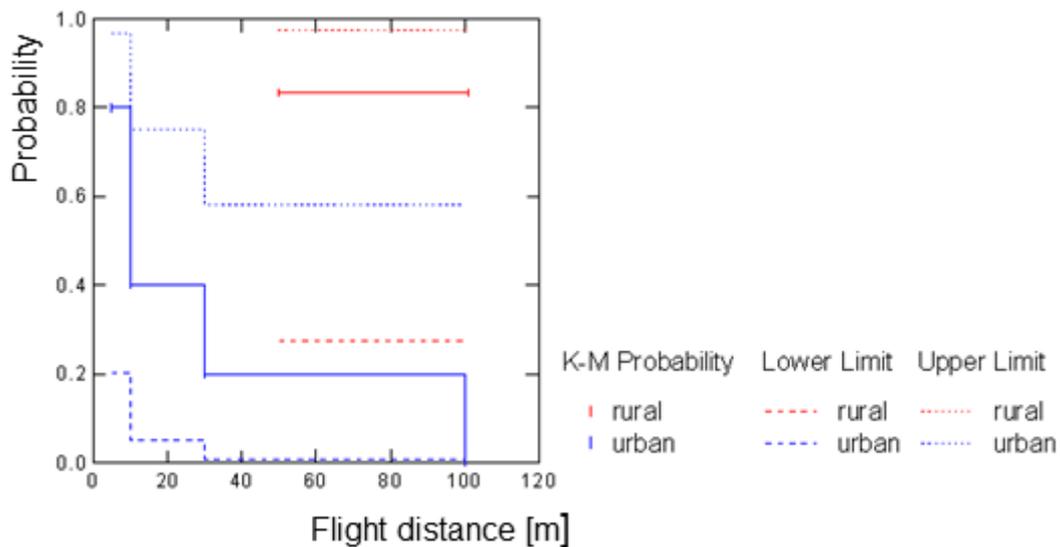


Fig. 3.3: Survival plot for flight distance of wild boar in urban and rural areas. Mean, probability for flight distances for urban wild boar ($n=5$) are displayed in blue, upper and lower limits are displayed with a dashed line. The probability for flight distances for wild boar in rural areas ($n=6$) are displayed in red, upper and lower probability limits are again displayed with dashed lines. The plot is the result of a Kaplan Meier survivorship analysis.

SECOND ORDER HABITAT SELECTION ANALYSIS: HOME RANGE LEVEL

The monthly home range size, as calculated by the 100 % minimum convex polygon (100 % mcp) approach, varied between 2 km² and 30 km², with 4.0 ± 2.5 km² (n = 28 months) for urban and 10.0 ± 6.0 km² (n = 36 months) for rural WB in our study area. The mean shift of monthly resting site centroids for urban WB was 250 ± 200 m (n = 28), rural WB shifted their resting sites on average by 1000 ± 800 m (n = 36) per month.

Differences in home range size (100% mcp per month and WB) depended on the landscape of fear (Tab. 3.2, Tab. S 6.3.2). The home range size of rural WB increased with increasing percentage of housing up to the maximum home range size of 30 km² in summer and a maximum of 10 km² in winter. Urban WB home range sizes did not change from summer to winter and were independent of the percentage of housing. There was no significant difference in the shift of the home range centroids between different months (model Inter; Tab. 3.2). The shift of the centre of the resting sites between months was not influenced by the spatial arrangement in terms of the landscapes of food or fear in either urban or rural WB, and best distinguished between urban and rural areas in the temporal domain by seasonal differences (Fig. 3.4): Whereas the monthly shift in resting sites increased in rural WB from 1000 ± 500 m (n = 15) in summer to 1500 ± 200 m (n = 21) in winter, urban WB showed a reverse pattern and reduced the monthly shift of resting sites from 450 ± 50 m (n = 19) in summer to 200 ± 150 m (n = 9) in winter.

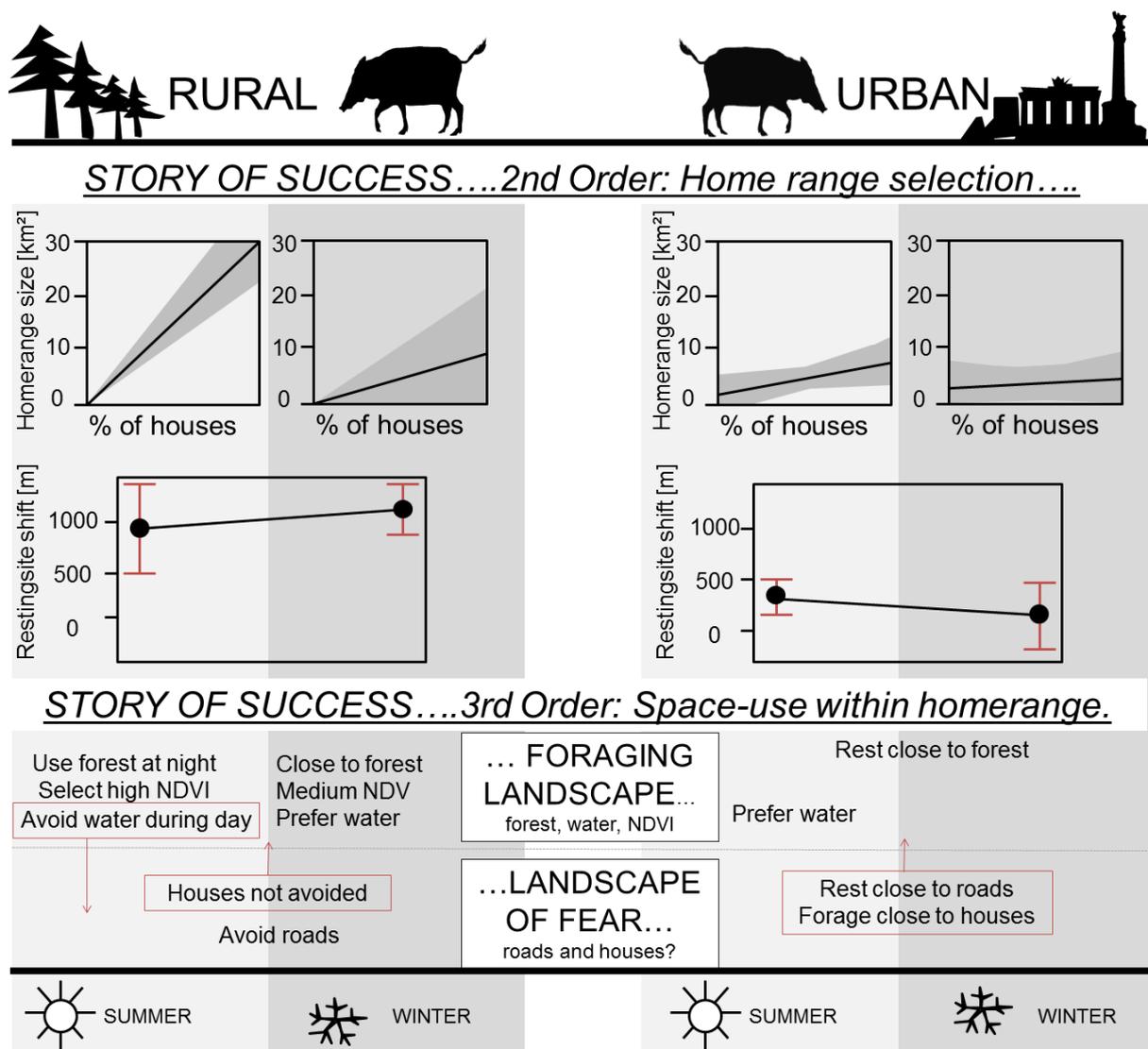
THIRD ORDER HABITAT SELECTION ANALYSIS – RESOURCE SELECTION BASED ON A MOVEMENT MODELLING APPROACH

The landscape of food was intensively used by WB. Both urban and rural WB selected locations with a high value of NDVI, representing high vegetation productivity. Urban WB selected locations close to forests and water bodies especially in summer (Fig. S 6.3.3A). Rural WB were more likely to be close to water bodies during winter, providing shelter and the opportunity to exploit this habitat as part of the landscape of food (Fig. S 6.3.3), whereas in summer they moved away during the day, since the water edge (“beach”) is used by humans for recreational purposes such as sun-bathing or swimming by people and therefore becomes a part of the landscape of fear. Urban WB were almost indifferent towards the landscape of fear (roads and housing), whereas rural WB used locations far away from roads but close to housing.

Tab. 3.2: The influence of landscape variables on home range size, use and movement characteristics of urban and rural WB. The influence of landscape variables in interaction with season (summer versus winter) and origin (urban versus rural) on home range size, home range shift, and resting sites shift as scaled response were studied with linear mixed models (LMMs). Predictor variables are defined and explained in Tab. 1. For the comparison of locations of WB and simulated movement tracks and for the comparison of WB locations at day (resting) and night (moving), generalized linear mixed models (GLMM) with logit link and binomial error structure were run, with individual identity of WB included as random effect. All variables were tested for interactions with season and origin. ‘Intercept’ stands for the intercept-only null model, the landscape-neutral model contained only season and origin but no landscape predictor variables. Shown here are the values for the Akaike Information Criterion with correction for finite sample size (AIC_c) and the difference ΔAIC_c to the ‘best’ model with the lowest AIC_c , for all models that fall within a range of 10 ΔAIC_c . The model weight (w) supplements the AIC model comparison by providing conditional probabilities for each model. A list of all candidate models is in Tab. S 6.3.1, Tab. S 6.3.2 and S 6.3.3 show full model selection tables.

Model name	model	df	logLik	AIC_c	ΔAIC_c	w
2nd order habitat analysis: home range						
<i>Numeric response: Home range size, n=54</i>						
Fear2	%Houses * Season * Origin	11	-41.06	110.71	0.00	1.00
<i>Numeric response variable: Distance of home range centroid shift, n=54</i>						
Inter	-	4	-66.81	142.46	0.00	0.86
Neutral	Season * Origin	7	-64.91	146.37	3.90	0.12
fear2	%Houses	1	-61.12	150.83	8.37	0.01
<i>Numeric response variable: Distance of resting site shift, n=54</i>						
Neutral	-	7	-65.11	146.76	0.00	0.58
Inter	Season * Origin	4	-69.41	147.67	0.91	0.37
Fear2	%Houses * Season * Origin	11	-61.81	152.23	5.46	0.04
3rd order analysis of space use: distance to important habitat variables						
<i>Binary response variable: comparison of GPS-locations of WB (1) and simulated movement tracks (0), n=469758</i>						
Full	(D_Forest +D_Water +NDVI*D_Houses+D_Roads)* Season * Origin	26	-187821.8	375695.6	0.00	1
<i>Binary response variable: comparison of GPS-locations of WB locations at day (resting, 0) and night (moving, 1), n= 78293</i>						
Full	(D_Forest +D_Water +NDVI*D_Houses +D_Roads)* Season * Origin	25	-37399.6	74849.2	0.00	1

Fig. 3.4: Results of second and third order habitat selection analysis in urban and rural wild boar in Berlin and Brandenburg. For the second order habitat selection analysis, effects plots from generalised linear mixed models for home range size in rural versus urban wild boars are shown in the upper part of the Fig.. The plots are separated for summer and winter since season was included as an interaction term in the best model. The effects plots for the shift of resting sites only separated between rural and urban groups, since the best model did not include habitat variables or seasonality. A summary of the effects for generalised linear mixed models (detailed effects plots in the electronic supplementary material, Fig. S 6.3.3) is shown for the third order habitat selection analysis. As binomial response, locations from wild boar (coded as 1) and simulated locations (coded as 0) and in a second model set day (= inactive times for WB, starting at 7am, coded as 0) and night (=active times for WB, starting at 7pm, coded as 1) were used. The tested variables were separated into variables representing the landscape of fear (distances to housing and roads) or the landscape of food (distances to forests and water bodies, NDVI).



The comparison of locations for resting and active behaviour showed a clear difference in the landscape of fear between rural and urban WB: Resting sites of urban WB were commonly located close to roads, sites which were avoided by rural conspecifics. Areas close to housing

were used by urban WB during active periods for foraging. Locations close to habitats that were part of the landscape of food such as forests and water bodies were used by urban WB especially when they rested. This demonstrated another modulation of behaviour from rural to urban WB, since rural WB showed a reverse pattern and went closer to forest and water bodies when they moved than during resting periods (Tab. 3.2, Tab. S 6.3.1). The vegetation productivity of habitats in the home ranges did not differ for resting and moving locations, but urban WB selected areas with a higher NDVI than rural WB.

Discussion

Our study provides the first scientific evidence that a large social mammalian herbivore trades off the fear caused by human disturbance with the need to access food in urban areas on two different spatial scales, as evidenced by hierarchical habitat selection analysis. On the home range scale, urban and rural WB differed in the placement of their home range on a spatial and temporal scale. Habitat use within the home range as evidenced by a detailed analysis of movements was dominated by the use of landscape of fear-related habitat structures for foraging and resting. The fact that only the landscape of fear variable ‘percentage of housing’ influenced the placement and size of the home range in rural WB, and that on the third order level of analysis urban WB used fear structures suggests that the perception of the landscape of fear was adjusted. While rural WB try to avoid the landscape of fear, urban WB focus on food and are more tolerant towards structures with a high level of human disturbance.

We predicted that urban WB should have smaller home ranges because of access to potentially food-rich habitats and that they would have to shift their home range more often than rural WB in response to the seasonal dynamics of human disturbance. Our results were consistent with the first prediction but we found no significant difference in the shift of home ranges. This is in line with results from studies on urban foxes (Janko *et al.* 2012) and urban WB from Cracow (Podgorski *et al.* 2013). The high individual variation in home range size is typical for WB (Keuling, Stier & Roth 2008). It is remarkable that both urban and rural WB showed no clear pattern in terms of shifting their home range centroids as observed for rural “field sows” (Keuling, Stier & Roth 2009) in northeast Germany. These “field sows” showed smaller home ranges because of access to food-rich patches and excellent conditions of shelter and a decreased risk of being hunted (Keuling, Stier & Roth 2009), conditions which appear to be comparable with conditions in our urban WB, and therefore explain why urban WB tend

to have smaller home ranges. The fact that rural WB had larger home ranges, especially when the percentage of housing is larger, is likely to be the result of ‘commuting’ behaviour, i.e. regular and predictable movements between two habitats such as forests and fields as previously observed in another study. Two individuals of our rural group showed such behaviour (IZW6, IZW7). Other individuals commuted between forests and built-up areas, especially during summer (IZW8). As a consequence, we might expect potential WB damage to habitats near built-up areas to increase during this season – as was observed in terms of WB damages close to housing in smaller villages in Brandenburg (HeikoWessendorf, Stadtforst Strausberg, personal communication). This demonstrates a modulation of the home range (= second order habitat selection) because of influences of the landscape of fear, here represented by the percentage of housing.

In general, animals are expected to first select the most profitable patches when they occupy new areas, as described by the ideal free distribution (Fretwell & Calver 1969). The fact that rural WB shifted their resting sites more than twice the distance of urban WB during summer and four times further during winter suggests that they commute, in this case between separate forest feeding locations. Alternatively, this may have been a response to the numerous drive hunts that take place especially in the rural parts of our study area during winter. Drive hunts can also lead to a dislocation of individuals and increase home range size (Calenge *et al.* 2002; Sodeikat & Pohlmeier 2003). Other explanations could be that urban WB might have fewer alternative profitable locations in the city or that they have already selected the most profitable patch. Urban WB could also be less influenced by the human landscape of fear and therefore might not need to adjust to the high level of dynamic change and instability of the city as observed in urban foxes (Doncaster & Macdonald 1991).

Urban WB home range sizes were not determined by landscape variables whereas rural WB increased their home range sizes in response to the dynamics of the landscape of fear. This might imply that rural WB avoid a crucial component of the landscape of fear by not touching areas close to housing. Yet the results of the finer-scale third order habitat selection analysis showed that areas close to housing were used. We therefore suggest that rural WB partly modulated the landscape of fear and commuted between forests and areas close to housing to forage (Lowry, Lill & Wong 2013). As urban WB were more likely to use locations close to housing at night when people are inactive, they effectively demonstrated that they can cope with human presence by an intelligent adjustment to the temporal pattern of human presence (and disturbance), similar to urban peccaries (*Tayassu tajacu*) which supplemented their diet

by visiting housing areas and decreased the distance to housing only when foraging (Bellantoni & Krausman 1993). Similar patterns of spatial avoidance were observed in urban bobcats and coyotes (Tigas, Van Vuren & Sauvajot 2002; George & Crooks 2006).

Although both rural and urban WB use areas close to housing for foraging, the higher density of houses in urban areas suggests that in practice the tolerance of human-related risk in urban WB might still exceed that of their rural conspecifics. Another hint that urban WB more closely adjusted to human induced disturbance and that the modulation of the landscape of fear was stronger than in rural WB is shown by their behaviour towards roads. Whereas rural WB avoid areas close to roads similar to other wildlife (Grinder & Krausman 2001; Dowding *et al.* 2010; Poessel *et al.* 2014; Thurfjell *et al.* 2015), urban WB used areas close to roads as resting sites. Areas close to roads are probably one of the safest locations for WB in urban areas. Urban WB used forest patches very intensely (Fig. 2) and stayed further away from forest at night when they foraged close to housing (Fig. 3). Urban forests in Berlin are particularly famous for their substantial numbers of visitors during the daytime (BDF 2015; Franusch 2015) which use the forest for recreational activities and therefore are part of the landscape of fear (Frid & Dill 2002; Ciuti *et al.* 2012). Birds for example avoid areas with high recreational activities in the forest (Rosner *et al.* 2014) and black bears (*Ursus americanus*) are more stressed close to human settlements and in the forest during the berry (collection) season than elsewhere when people visited the forest more frequently (Stoen *et al.* 2015).

In our urban study area there are numerous domestic dog exercising areas where private people or professional dog walkers go for walks with groups of up to 10 dogs (Andreas Constien, forester in the Grunewald, personal communication). From an evolutionary point of view, since the ancestors of domestic dogs were wolves hunting WB if available (Nores, Llaneza & Alvarez 2008) we should expect that WB recognise predators and incorporate measures of predator presence in their assessment of habitats as part of their landscape of fear. Within rural Brandenburg, domestic dogs are employed in WB hunting to this day (Sodeikat & Pohlmeier 2003), and should therefore be recognised as a potential predator and a prime source of disturbance which enhances and modifies the spatial distribution of risk within the landscape of fear, since domestic dogs will readily enter and move throughout a habitat and are not limited to structures such as roads as people usually are. Since people walking their domestic dogs prefer to enter sites within the forest where they usually take their dogs off the leash, areas close to major roads are probably safer for WB. Here they are less likely to be

detected by people and their dogs, since dogs are also frequently restricted in their movements because they are led on a leash (personal observations). Rural forests are much less frequented by people and their domestic dogs than urban forests and therefore provide a safer landscape of food with little disturbance. Rural WB can therefore select hiding places within the rural forest and avoid roads. Black bears (*Ursus americanus*) even distinguish between paved main roads and forest roads and adjust their movement to the changes in the spatial distribution of increasing hunting risk these entail (Stillfried *et al.* 2015). It is possible that WB also distinguish between different risk levels related to roads and adjust their behaviour accordingly.

Rural WB avoided areas close to water bodies during the summer and preferred areas close to water bodies in winter, whereas urban WB preferred areas close to water bodies during summer. Water bodies in both urban and rural forests are used by many people for recreational activities such as swimming, particularly during the summer. Rural WB avoid these patches during the summer because of the human induced landscape of fear (Frid & Dill 2002; Ciuti *et al.* 2012; Rosner *et al.* 2014; Stoen *et al.* 2015), whereas during the winter when the number of drive hunts in the rural forests is high, they select areas close to water bodies as hiding places. Urban WB were located close to common recreational beaches inside reedbeds during the day in summer. These observations not only demonstrate how WB adjust their landscape of fear, they are also consistent with their significant reduction in flight distances and are in line with observations about reduced flight distances in other urban animals (Bateman & Fleming 2014; Gravalin, Key & Lill 2014).

In conclusion, urban WB modulated their landscape of fear in order to avail themselves of the new opportunities which the urban environment offers and to efficiently and appropriately manage the trade-off between access to food and the avoidance of predators. They selected areas close to roads as resting sites since they learnt that the disturbance by cars is less risky than the disturbance by human recreational activities in urban forests. They also used areas close to water and human recreational swimming beaches because they reduced their flight distance from people and adjusted to human proximity. By matching their activity patterns to periods of relative human inactivity, urban WB foraged in areas close to housing at night. Overall, the study details for the first time how a large social ungulate assesses the spatial and temporal landscape in terms of access to food and risk and how this assessment is adjusted in a habitat-specific manner in terms of their concomitant use in urban areas. The fact that at the spatial scale of second order habitat selection analysis only the landscape of fear appears

modulated whereas we find a complex and context-dependent pattern at the more detailed spatial scale of third order habitat selection analyses shows that urban WB are able to measure fine scale changes of spatio-temporal patterns within their home ranges. A combination of the understanding of the characteristics of habitats and the flexibility in their behaviour allows them to succeed even in human dominated urban environments.

Acknowledgements

We thank Andreas Burchardt, Andreas Constien, Egbert Gleich, Erica Grant, Bodo Janitza, Uwe Peschke, Marion Schmolke and Heiko Wessendorf for their help with trapping wild boar, the Leibniz Centre for Agricultural Landscape Research (ZALF) and Hinrich Zoller for providing traps, Anne Berger and Knut Eichhorn for the use of telemetry devices, Matthias Busch, Pierre Gras and Ilja Heckmann for assistance with data analyses and National Geographic, the “Stiftung Naturschutz” and the Leibniz Institute for Zoo & Wildlife Research for funding.

References

- Amici, A., Serrani, F., Rossi, C.M. & Primi, R. (2012) Increase in crop damage caused by wild boar (*Sus scrofa* L.): the "refuge effect". *Agronomy for Sustainable Development*, **32**, 683-692.
- Dog areas, S.B.M.o.d.e. <http://www.stadtentwicklung.berlin.de/forsten/hundeauslauf/>.
- Austin, M.P. (2002) Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. *Ecological Modelling*, **157**, 101-118.
- Baker, P.J., Bentley, A.J., Ansell, R.J. & Harris, S. (2005) Impact of predation by domestic cats *Felis catus* in an urban area. *Mammal Review*, **35**, 302-312.
- Bateman, P.W. & Fleming, P.A. (2012) Big city life: carnivores in urban environments. *Journal of Zoology*, **287**, 1-23.
- Bateman, P.W. & Fleming, P.A. (2014) Does human pedestrian behaviour influence risk assessment in a successful mammal urban adapter? *Journal of Zoology*, **294**, 93-98.
- B.D.F. (2015) <https://www.berlin.de/tourismus/nachrichten/3688703-1721038-grunewald-ist-waldgebiet-des-jahres-2015>.
- Bellantoni, E.S. & Krausman, P.R. (1993) Habitat use by collared peccaries in an urban-environment. *Southwestern Naturalist*, **38**, 345-351.
- Beninde, J., Veith, M. & Hochkirch, A. (2015) Biodiversity in cities needs space: a meta-analysis of factors determining intra-urban biodiversity variation. *Ecology Letters*, **18**, 581-592.
- Bino, G., Levin, N., Darawshi, S., Van Der Hal, N., Reich-Solomon, A. & Kark, S. (2008) Accurate prediction of bird species richness patterns in an urban environment using Landsat-derived NDVI and spectral unmixing. *International Journal of Remote Sensing*, **29**, 3675-3700.

- Bonnot, N., Morellet, N., Verheyden, H., Cargnelutti, B., Lourtet, B., Klein, F. & Hewison, A.J.M. (2013) Habitat use under predation risk: hunting, roads and human dwellings influence the spatial behaviour of roe deer. *European Journal of Wildlife Research*, **59**, 185-193.
- Borowik, T., Pettorelli, N., Soennichsen, L. & Jedrzejska, B. (2013) Normalized difference vegetation index (NDVI) as a predictor of forage availability for ungulates in forest and field habitats. *European Journal of Wildlife Research*, **59**, 675-682.
- Boyce, M.S. (2006) Scale for resource selection functions. *Diversity and Distributions*, **12**, 269-276.
- Boyce, M.S., Vernier, P.R., Nielsen, S.E. & Schmiegelow, F.K.A. (2002) Evaluating resource selection functions. *Ecological Modelling*, **157**, 281-300.
- Brown, J.S., Laundre, J.W. & Gurung, M. (1999) The ecology of fear: Optimal foraging, game theory, and trophic interactions. *Journal of Mammalogy*, **80**, 385-399.
- Cahill, S., Llimona, F., Cabaneros, L. & Calomardo, F. (2012) Characteristics of wild boar (*Sus scrofa*) habituation to urban areas in the Collserola Natural Park (Barcelona) and comparison with other locations. *Animal Biodiversity and Conservation*, **35**, 221-233.
- Cahill, S., Llimona, F. & Gracia, J. (2003) Spacing and nocturnal activity of wild boar *Sus scrofa* in a Mediterranean metropolitan park. *Wildlife Biology*, **9**, 3-13.
- Calenge, C. (2006) The package "adehabitat" for the R software: A tool for the analysis of space and habitat use by animals. *Ecological Modelling*, **197**, 516-519.
- Calenge, C., Maillard, D., Vassant, J. & Brandt, S. (2002) Summer and hunting season home ranges of wild boar (*Sus scrofa*) in two habitats in France. *Game & Wildlife Science*, **19**, 281-301.
- Chiari, M., Ferrari, N., Bertoletti, M., Avisani, D., Cerioli, M., Zanoni, M., Alborali, L.G., Lanfranchi, P., Lelli, D., Martin, A.M. & Antonio, L. (2015) Long-Term Surveillance of Aujeszky's Disease in the Alpine Wild Boar (*Sus scrofa*). *Ecohealth*, **12**, 563-570.
- Ciuti, S., Northrup, J.M., Muhly, T.B., Simi, S., Musiani, M., Pitt, J.A. & Boyce, M.S. (2012) Effects of Humans on Behaviour of Wildlife Exceed Those of Natural Predators in a Landscape of Fear. *Plos One*, **7**, 13.
- Cousse, S., Janeau, G., Spitz, F., Priede, I.G. & Swift, S.M. (1992) "Telemetry on free-ranging wild boars (*Sus scrofa* L.): temporal and spatial structure of daily movements." *Priede IG & Swift SM, Edits. Wildlife telemetry. London: Ellis Horwood* 693-697.
- Dardaillon, M. & Beugnon, G. (1987) The influence of some environmental characteristics on the movements of wild boar *sus-scrofa*. *Biology of Behaviour*, **12**, 82-92.
- Davison, J., Huck, M., Delahay, R.J. & Roper, T.J. (2008) Urban badger setts: characteristics, patterns of use and management implications. *Journal of Zoology*, **275**, 190-200.
- Dinter, U. (1991) Das Raum-Zeitverhalten von Schwarzwild im Grunewald in den Sommermonaten unter besonderer Berücksichtigung menschlicher Störungen, Dissertation, Ludwig-Maximilian-Universität
- Doncaster, C.P. & Macdonald, D.W. (1991) Drifting territoriality in the red fox *vulpes-vulpes*. *Journal of Animal Ecology*, **60**, 423-439.
- Dowding, C.V., Harris, S., Poulton, S. & Baker, P.J. (2010) Nocturnal ranging behaviour of urban hedgehogs, *Erinaceus europaeus*, in relation to risk and reward. *Animal Behaviour*, **80**, 13-21.
- Fernández, N., Kramer-Schadt, S. & Thulke, H.-H. (2006) Viability and risk assessment in species restoration: planning reintroductions for the wild boar, a potential disease reservoir. *Ecology and Society* 11.1
- Ficetola, G.F., Bonardi, A., Mairota, P., Leronni, V. & Padoa-Schioppa, E. (2014) Predicting wild boar damages to croplands in a mosaic of agricultural and natural areas. *Current Zoology*, **60**, 170-179.
- Franusch, M. (2015) Der Berliner Grunewald ist der Wald des Jahres 2015. (ed. A. Kögel). Der Tagesspiegel, 22.3.2015.
- Fretwell, S.D. & Calver, J.S. (1969) On territorial behavior and other factors influencing habitat distribution in birds. *Acta biotheoretica*, **19**, 37-44.
- Frid, A. & Dill, L. (2002) Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology*, **6** (1):11.

- Gehrt, S.D., Anchor, C. & White, L.A. (2009) Home range and landscape use of coyotes in a metropolitan landscape: conflict or coexistence? *Journal of Mammalogy*, **90**, 1045-1057.
- George, S.L. & Crooks, K.R. (2006) Recreation and large mammal activity in an urban nature reserve. *Biological Conservation*, **133**, 107-117.
- Gloor, S., Bontadina, F., Hegglin, D., Deplazes, P. & Breitenmoser, U. (2001) The rise of urban fox populations in Switzerland. *Mammalian Biology*, **66**, 155-164.
- Gravolin, I., Key, M. & Lill, A. (2014) Boldness of urban Australian magpies and local traffic volume. *Avian Biology Research*, **7**, 244-250.
- Gray, M., Wilmers, C.C., Reed, S.E. & Merenlender, A.M. (2016) Landscape feature-based permeability models relate to puma occurrence. *Landscape and Urban Planning*, **147**, 50-58.
- Grinder, M.I. & Krausman, P.R. (2001) Home range, habitat use, and nocturnal activity of coyotes in an urban environment. *Journal of Wildlife Management*, **65**, 887-898.
- Hastie, T. & Tibshirani, R. (1987) Generalized additive-models - some applications. *Journal of the American Statistical Association*, **82**, 371-386.
- Hespeler, B. (2007) Leitlinie Jagd im urbanen Raum von Berlin. *Senatsverwaltung fuer Stadt und Umwelt, Berliner Forsten*.
- Hughes, J. & Macdonald, D.W. (2013) A review of the interactions between free-roaming domestic dogs and wildlife. *Biological Conservation*, **157**, 341-351.
- Janeau, G., Cousse, S., Cargnelutti, B. & Spitz, F. (1995) Role of daily movements in the sociospatial organization of wild boar populations (*Sus scrofa* L). *Revue D Ecologie-La Terre Et La Vie*, **50**, 35-48.
- Janko, C., Schroder, W., Linke, S. & Konig, A. (2012) Space use and resting site selection of red foxes (*Vulpes vulpes*) living near villages and small towns in Southern Germany. *Acta Theriologica*, **57**, 245-250.
- Jansen, A., Luge, E., Guerra, B., Wittschen, P., Gruber, A.D., Loddenkemper, C., Schneider, T., Lierz, M., Ehlert, D., Appel, B., Stark, K. & Noeckler, K. (2007) Leptospirosis in urban wild boars, Berlin, Germany. *Emerging Infectious Diseases*, **13**, 739-742.
- Jarolimek, J., Vanek, J., Jezek, M., Masner, J. & Stoces, M. (2014) The telemetric tracking of wild boar as a tool for field crops damage limitation. *Plant Soil and Environment*, **60**, 418-425.
- Johnson, C.J., Nielsen, S.E., Merrill, E.H., McDonald, T.L. & Boyce, M.S. (2006) Resource selection functions based on use-availability data: Theoretical motivation and evaluation methods. *Journal of Wildlife Management*, **70**, 347-357.
- Johnson, D.H. (1980) The comparison of usage and availability measurements for evaluating resource preference. *Ecology*, **61**, 65-71.
- Kertson, B.N., Spencer, R.D., Marzluff, J.M., Hepinstall-Cymerman, J. & Grue, C.E. (2011) Cougar space use and movements in the wildland-urban landscape of western Washington. *Ecological Applications*, **21**, 2866-2881.
- Keuling, O., Stier, N. & Roth, M. (2008) Annual and seasonal space use of different age classes of female wild boar *Sus scrofa* L. *European Journal of Wildlife Research*, **54**, 403-412.
- Keuling, O., Stier, N. & Roth, M. (2009) Commuting, shifting or remaining? Different spatial utilisation patterns of wild boar *Sus scrofa* L. in forest and field crops during summer. *Mammalian Biology*, **74**, 145-152.
- Keuling, O., Strauss, E. & Siebert, U. (2016) Regulating wild boar populations is "somebody else's problem"! - Human dimension in wild boar management. *Science of the Total Environment*, **554**, 311-319.
- Klar, N., Fernandez, N., Kramer-Schadt, S., Herrmann, M., Trinzen, M., Buttner, I. & Niemitz, C. (2008) Habitat selection models for European wildcat conservation. *Biological Conservation*, **141**, 308-319.
- Laundre J. W., Hernandez L. & Ripple W. J. (2010) The Landscape of Fear: Ecological Implications of Being Afraid. *The Open Ecological Journal*, **3**, 1-7.
- Laundre, J.W., Hernandez, L., Lopez Medina, P., Campanella, A., Lopez-Portillo, J., Gonzalez-Romero, A., Grajales-Tam, K.M., Burke, A.M., Gronemeyer, P. & Browning, D.M. (2014) The

- landscape of fear: the missing link to understand top-down and bottom-up controls of prey abundance? *Ecology*, **95**, 1141-1152.
- Laznik, Z. & Trdan, S. (2014) Evaluation of different soil parameters and wild boar (*Sus scrofa* L.) grassland damage. *Italian Journal of Animal Science*, **13**, 7.
- Lowry, H., Lill, A. & Wong, B.B.M. (2013) Behavioural responses of wildlife to urban environments. *Biological Reviews*, **88**, 537-549.
- Magle, S.B., Hunt, V.M., Vernon, M. & Crooks, K.R. (2012) Urban wildlife research: Past, present, and future. *Biological Conservation*, **155**, 23-32.
- Magle, S.B., Simoni, L.S., Lehrer, E.W. & Brown, J.S. (2014) Urban predator-prey association: coyote and deer distributions in the Chicago metropolitan area. *Urban Ecosystems*, **17**, 875-891.
- Maibeche, Y., Moali, A., Yahi, N. & Menard, N. (2015) Is Diet Flexibility an Adaptive Life Trait for Relictual and Peri-Urban Populations of the Endangered Primate *Macaca sylvanus*? *Plos One*, **10**, 22.
- Manly, B.F.J., McDonald, L.L., Thomas, D.L., McDonald, T.L., Erickson, W.P., Manly, B.F.J., McDonald, L.L., Thomas, D.L., McDonald, T.L. & Erickson, W.P. (2002) Resource selection by animals: statistical design and analysis for field studies. *Springer Science & Business Media, Second edition*.
- Massei, G., Kindberg, J., Licoppe, A., Gacic, D., Sprem, N., Kamler, J., Baubet, E., Hohmann, U., Monaco, A., Ozolins, J., Cellina, S., Podgorski, T., Fonseca, C., Markov, N., Pokorny, B., Rosell, C. & Nahlik, A. (2015) Wild boar populations up, numbers of hunters down? A review of trends and implications for Europe. *Pest Management Science*, **71**, 492-500.
- McKinney, M.L. (2002) Urbanization, biodiversity, and conservation. *Bioscience*, **52**, 883-890.
- Morelle, K., Lehaire, F. & Lejeune, P. (2013) Spatio-temporal patterns of wildlife-vehicle collisions in a region with a high-density road network. *Nature Conservation-Bulgaria*, 53-73.
- Morelle, K., Lehaire, F. & Lejeune, P. (2014) Is wild boar heading towards movement ecology? A review of trends and gaps. *Wildlife Biology*, **20**, 196-205.
- Morelle, K., Podgorski, T., Prevot, C., Keuling, O., Lehaire, F. & Lejeune, P. (2015) Towards understanding wild boar *Sus scrofa* movement: a synthetic movement ecology approach. *Mammal Review*, **45**, 15-29.
- Murray, M., Cembrowski, A., Latham, A.D.M., Lukasik, V.M., Pruss, S. & St Clair, C.C. (2015) Greater consumption of protein-poor anthropogenic food by urban relative to rural coyotes increases diet breadth and potential for human-wildlife conflict. *Ecography*, **38**, 1235-1242.
- Murray, M.H. & St Clair, C.C. (2015) Individual flexibility in nocturnal activity reduces risk of road mortality for an urban carnivore. *Behavioral Ecology*, **26**, 1520-1527.
- Nores, C., Llana, L. & Alvarez, M.A. (2008) Wild boar *Sus scrofa* mortality by hunting and wolf *Canis lupus* predation: an example in northern Spain. *Wildlife Biology*, **14**, 44-51.
- Otoni, I., de Oliveira, F.F.R. & Young, R.J. (2009) Estimating the diet of urban birds: The problems of anthropogenic food and food digestibility. *Applied Animal Behaviour Science*, **117**, 42-46.
- Podgorski, T., Bas, G., Jedrzejewska, B., Soennichsen, L., Sniezko, S., Jedrzejewski, W. & Okarma, H. (2013) Spatiotemporal behavioral plasticity of wild boar (*Sus scrofa*) under contrasting conditions of human pressure: primeval forest and metropolitan area. *Journal of Mammalogy*, **94**, 109-119.
- Poessel, S.A., Burdett, C.L., Boydston, E.E., Lyren, L.M., Alonso, R.S., Fisher, R.N. & Crooks, K.R. (2014) Roads influence movement and home ranges of a fragmentation-sensitive carnivore, the bobcat, in an urban landscape. *Biological Conservation*, **180**, 224-232.
- Rosner, S., Mussard-Forster, E., Lorenc, T. & Muller, J. (2014) Recreation shapes a "landscape of fear" for a threatened forest bird species in Central Europe. *Landscape Ecology*, **29**, 55-66.
- Sodeikat, G. & Pohlmeier, K. (2003) Escape movements of family groups of wild boar *Sus scrofa* influenced by drive hunts in Lower Saxony, Germany. *Wildlife Biology*, **9**, 43-49.
- Stillfried, M., Belant, J.L., Svoboda, N.J., Beyer, D.E. & Kramer-Schadt, S. (2015) When top predators become prey: black bears alter movement behaviour in response to hunting pressure. *Behavioural Processes*, **120**, 30-39.

- Stoen, O.G., Ordiz, A., Evans, A.L., Laske, T.G., Kindberg, J., Frobert, O., Swenson, J.E. & Arnemo, J.M. (2015) Physiological evidence for a human-induced landscape of fear in brown bears (*Ursus arctos*). *Physiology & Behavior*, **152**, 244-248.
- Tennekes, M. (2016) Tab.plot, a Visualization of Large Datasets, Version 1.3. Package.
- Theimer, T.C., Clayton, A.C., Martinez, A., Peterson, D.L. & Bergman, D.L. (2015) Visitation rate and behavior of urban mesocarnivores differs in the presence of two common anthropogenic food sources. *Urban Ecosystems*, **18**, 895-906.
- Thurfjell, H., Spong, G. & Ericsson, G. (2013) Effects of hunting on wild boar *Sus scrofa* behaviour. *Wildlife Biology*, **19**, 87-93.
- Thurfjell, H., Spong, G. & Ericsson, G. (2014) Effects of weather, season, and daylight on female wild boar movement. *Acta Theriologica*, **59**, 467-472.
- Thurfjell, H., Spong, G., Olsson, M. & Ericsson, G. (2015) Avoidance of high traffic levels results in lower risk of wild boar-vehicle accidents. *Landscape and Urban Planning*, **133**, 98-104.
- Tigas, L.A., Van Vuren, D.H. & Sauvajot, R.M. (2002) Behavioral responses of bobcats and coyotes to habitat fragmentation and corridors in an urban environment. *Biological Conservation*, **108**, 299-306.
- Tryjanowski, P., Skorka, P., Sparks, T.H., Biadun, W., Brauze, T., Hetmanski, T., Martyka, R., Indykiewicz, P., Myczko, L., Kunysz, P., Kawa, P., Czyz, S., Czechowski, P., Polakowski, M., Zduniak, P., Jerzak, L., Janiszewski, T., Golawski, A., Dudus, L., Nowakowski, J.J., Wuczynski, A. & Wysocki, D. (2015) Urban and rural habitats differ in number and type of bird feeders and in bird species consuming supplementary food. *Environmental Science and Pollution Research*, **22**, 15097-15103.
- Valeix, M., Hemson, G., Loveridge, A.J., Mills, G. & Macdonald, D.W. (2012) Behavioural adjustments of a large carnivore to access secondary prey in a human-dominated landscape. *Journal of Applied Ecology*, **49**, 73-81.
- Wagenmakers, E.-J. & Farrell, S. (2004) AIC model selection using Akaike weights. *Psychonomic bulletin & review*, **11**, 192-196.
- White, P.C.L., Saunders, G. & Harris, S. (1996) Spatio-temporal patterns of home range use by foxes (*Vulpes vulpes*) in urban environments. *Journal of Animal Ecology*, **65**, 121-125.
- Wood, S.N. (2004) Suitable and efficient multiple smoothing parameter estimation for generalized additive models. *Journal of the American Statistical Association*, **99**, 673-686.

CHAPTER 4: Manuscript 3

Wild Boar Nutrition

Wild inside: Urban Wild Boar select natural, not anthropogenic food resources.

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A revised version of this manuscript is now published with PLOS ONE
(<https://doi.org/10.1371/journal.pone.0175127>)

Author's contribution statement

Conceptual framework and predictions of this study were discussed and developed by Milena Stillfried (MS), Stephanie Kramer-Schadt (SKS) and Sylvia Ortmann (SO).

MS and Konstantin Börner (KB) collected samples. MS conducted laboratory analyses, MB and MS prepared maps of landscape variables, MS and PG conducted statistical analyses, MS wrote the manuscript which was extensively commented on and edited by SO, SKS and PG.

Wild inside: Urban Wild Boar select natural, not anthropogenic food resources.

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Abstract

Most wildlife species are urban avoiders, but some became urban utilizers and dwellers successfully living in cities. Often, they are assumed to be attracted into urban areas by easy accessible and highly energetic anthropogenic food sources. We macroscopically analysed stomachs of 265 wild boar (*Sus scrofa*, hereafter WB) from urban areas (hereafter ‘city WB’), urban forests (hereafter ‘urban forest WB’) and the surrounding countryside (hereafter ‘rural WB’). From the stomach contents we determined modulus of fineness (MOF), amount of acid insoluble ash (AIA), energy and macronutrients such as protein, fat, fibre and starch. We found only few cases of anthropogenic food in the qualitative macroscopic analysis. We categorized the WB into five stomach content categories and into four clusters of different genetic origin. We run linear mixed models to test: (1) differences in the proportion of landscape variables (2) differences of nutrients consumed within clusters and stomach categories and (3) the impact of landscape variables on ingested nutrients.

We found differences among the different landscapes, because rural areas are dominated by forests, agriculture and smaller villages while human associated landscape variables such as percentage of houses are most dominant in the city. The analysis of landscape variables revealed that greenland, agriculture and forest had a stronger influence on the nutrient

composition of WB stomachs than human associated landscape variables such as human density or percentage of houses.

Anthropogenic food such as garbage might serve as fallback food when access to natural resources is limited. We infer that city WB became tolerant to disturbance by human urbanites, while foraging abundant, natural resources. WB might use anthropogenic resources if those are easier to exploit and more abundant than natural resources – a characteristic behaviour of omnivores.

Key words: Energy, *Sus scrofa*, nutrient analysis, acorn, genetic cluster, human wildlife conflict, urban ecology, Berlin

Introduction

Urban areas are expanding worldwide, thereby fragmenting habitats and threatening biodiversity (Seto *et al.* 2011). While urban avoiders (McKinney 2002; Fischer *et al.* 2015) are “losers” of urbanization, urban utilizers and dwellers (McKinney 2002; Fischer *et al.* 2015) succeed even in cities where artificial landscape structures (Lowry, Lill & Wong 2013) such as sealed surfaces lead to a decrease in biodiversity (Beninde, Veith & Hochkirch 2015). In addition to alterations in the landscape, urban animals have to deal with a human disturbance level (Frid & Dill 2002; Ciuti *et al.* 2012) which is often location-specific, with animals being able to distinguish spatial variations in risk (Bonnot *et al.* 2013; Rosner *et al.* 2014; Stillfried *et al.* 2015). To succeed in urban areas, animals have to trade-off between access to food and predator avoidance including anthropogenic disturbance (Pierce & Ollason 1987; Brown, Laundre & Gurung 1999). Increasing the tolerance towards disturbances is one way of trading-off fear vs. food and can be determined by ecological, behavioural, and physiological characteristics such as home range area, population density, metabolic rate, movement speed, transport costs, and ingestion rate (Milne *et al.* 1992).

Optimal access to food depends on type of food choice, optimal patch choice, and time management (Emlen 1966; MacArthur & Pianka 1966; Charnov 1976; Pyke, Pulliam & Charnov 1977; Krebs 1978; Pyke 1984) and are changed in urban areas according to resource availability: Urban landscapes provide natural as well as anthropogenic food sources (e.g.

garbage). Green areas in cities might harbour a high biodiversity (Beninde, Veith & Hochkirch 2015), which provide natural foods together with street trees or forest patches in cities (Nowak *et al.* 2001; Pauleit *et al.* 2002). While studies showing the impact of natural food sources on the diet of urban animals are rare, numerous studies describe the impact of anthropogenic food and garbage (Hafeez *et al.* 2011; Cahill *et al.* 2012; Börner & Olbertz 2014; Lewis *et al.* 2015; Murray *et al.* 2015). Anthropogenic food sources are easily accessible (Cahill *et al.* 2012; Murray *et al.* 2015; Theimer *et al.* 2015; Tryjanowski *et al.* 2015) and provide a high amount of energy (Ottoni, de Oliveira & Young 2009; Maibeche *et al.* 2015). Consuming anthropogenic food increases for example dietary breadth (Murray *et al.* 2015; Theimer *et al.* 2015). Increased food availability in urban areas can also lead to lower seasonal constraints, resulting in a population growth and further expansion into cities (Maibeche *et al.* 2015). Stomach content analyses revealed that human-associated food supply was sufficient to feed a much higher number of animals than currently present, which could explain a continual increase of urban population densities (Contesse *et al.* 2004). In other studies, an inter- and intra-annual variation of foraging pattern was observed: extensive foraging in urban areas when natural food production was poor and a switch to natural food sources, when available (Lewis *et al.* 2015). To sum up, urban habitats may provide diverse food sources, where especially opportunistic foragers can benefit from.

The WB is an omnivorous species with a flexible diet being herbivorous, predacious and granivorous simultaneously (Ballari & Barrios-Garcia 2014). As a versatile forager it displays four main feeding behaviours: browsing and grazing, foraging on the ground, rooting and predation (Ballari & Barrios-Garcia 2014). Foraging WB often get into conflicts with humans, as it causes intense damage to crops (Herrero *et al.* 2006; Amici *et al.* 2012; Frackowiak *et al.* 2013; Ficetola *et al.* 2014; Nasiadka & Janiszewski 2015) and greenlands (Welandar 2000; Bueno *et al.* 2009; Laznik & Trdan 2014). WB prefer plant matter over animal matter (Schley & Roper 2003; Herrero *et al.* 2006; Ballari & Barrios-Garcia 2014) with a special preference of highly digestible and nutritious food such as acorn (*Quercus humilis*, Herrero *et al.* 2005). Among agricultural crops the preferred food of WB is maize (*Zea maize*, Herrero *et al.* 2006). In general, seasonal, inter-annual and regional differences in the diet indicate that WB feed on different food types according to availability (Schley & Roper 2003). Since food availability in urban and rural areas differs due to the high availability of anthropogenic food in urban areas (Hafeez *et al.* 2011; Cahill *et al.* 2012; Börner & Olbertz 2014; Lewis *et al.* 2015;

Murray *et al.* 2015), we expect to find significant differences in the diet of WB from different urban and rural areas.

WB in Barcelona are regularly fed in urban areas (Cahill *et al.* 2012) while in Berlin direct feeding of wild boar is rare (Kotulski & König 2008). The Senate of Berlin forbade wildlife feeding, but the effect of this action on WB foraging pattern remains unknown as no monitoring scheme is implemented to date. Therefore, we conducted the first study comparing diets of WB along an urban-rural gradient.

Here we compared the diet of WB in four different groups, each living in a distinguishable environment differing in the percentage of sealed surfaces, houses, human population density, percentage of coniferous and deciduous forest and percentage of agriculture and greenland: Two groups of urban forest WB were compared to WB from rural Brandenburg and WB from the city of Berlin (shot by city hunters). We hypothesize that the diet of WB from different origins– differs and that the diet reflects the availability of local characteristic resources of respective food patches.

We predicted that

- (5) the amount of anthropogenic food sources is highest in stomachs of city WB;
- (6) different macroscopic stomach content types are not equally frequent within city-WB, urban forest-WB and rural-WB because they mirror different forest and landscape compositions;
- (7) amount of nutrients and energy are expected to be highest in stomachs of city WB and in stomach with maize and acorn;
- (8) landscape structures influence energetic value and quality of food.

Material and Methods:

STUDY AREA AND SAMPLE COLLECTION

The study was conducted in Berlin (52°31'N, 13°24'E) and surrounding areas of the Federal State Brandenburg (Fig. 4.1). Twenty percent of the area of Berlin was covered with forests, divided into four main forests. The forest of the western part of Berlin (including the Grunewald, GW) was reforested with mixed trees (pine *Pinus sylvestris*, oak *Quercus robur*, *Quercus rubra*, beech *Fagus sylvatica*) after the second world war and afterwards used as recreational forest (Berlin 2015). The eastern part of the Berlin forest (including Koepenick,

KO) and the forests in Brandenburg (BB) are covered with coniferous forests, dominated by pine (*Pinus sylvestris*). Between 2012 and 2015 we collected stomachs of 265 individuals (Fig. 4.1) and stored samples frozen at -20° . Samples from the city boar were obtained from single hunts carried out by ‘city hunters’ and all other wild boar samples were from large battue hunts in the urban and rural forests. Genetic samples were collected from the same study area (Stillfried *et al.* 2016).

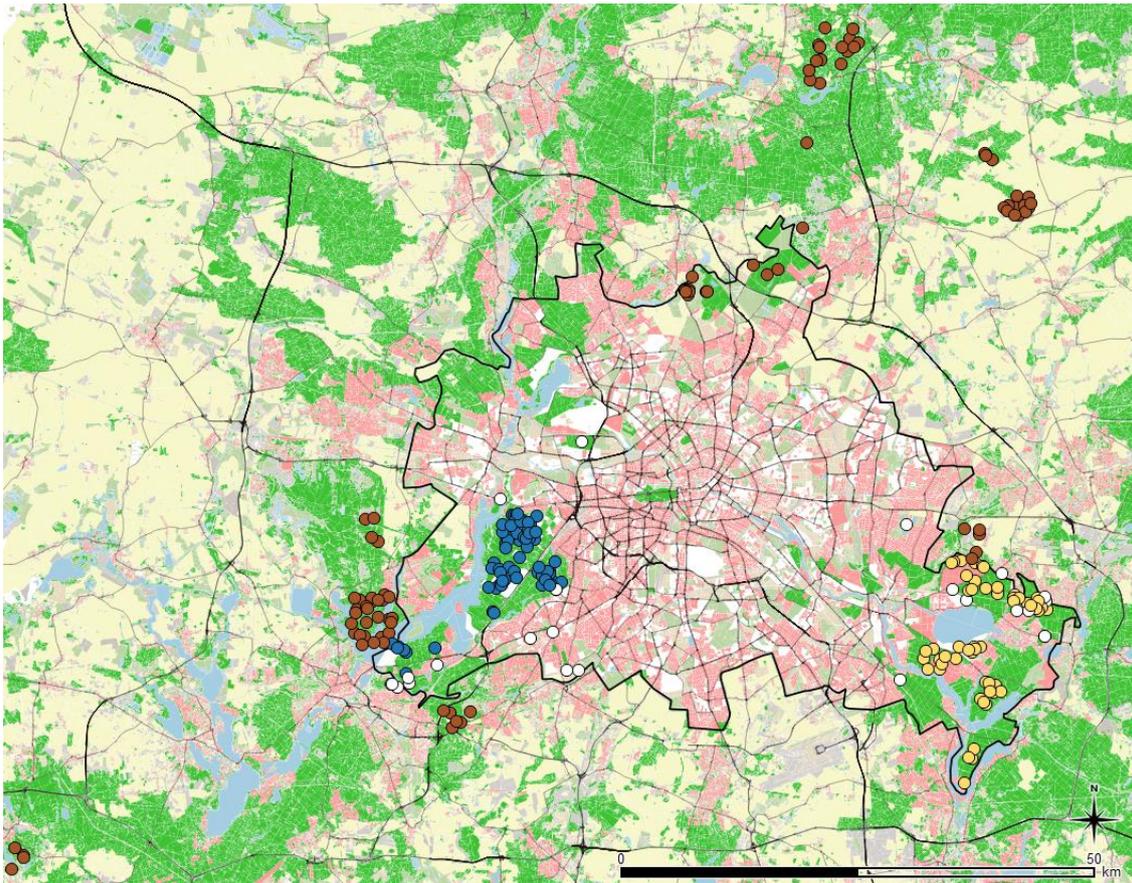


Fig. 4.1: Study area including sample locations for wild boar stomachs in Berlin and Brandenburg between 2012 and 2015. The different colors of the sample locations refer to the sample origin: Two urban forests, Grunewald (dark blue dots, Sample size, $n=69$) and Koenigswald (yellow dots, $n=56$), the city of Berlin (white dots, $n=26$) and rural Brandenburg (brown dots, $n=96$) are divided. The black line shows the border of Berlin. Background map: Habitat map of Berlin and Brandenburg, Stillfried *et al.* in prep, Chapter 3.

MACROSCOPIC ANALYSIS

For the macroscopic content analysis, the stomach content was spread in a 30x40cm bowl and searched for macroscopically identifiable food residues. All single food residues were recorded qualitatively with help of a checklist. Based on the most dominant food items found,

the stomachs were categorized in 5 categories. A representative subsample of each stomach-content was separated for subsequent laboratory analyses.

LABORATORY PROCEDURE

To determine the particle size and macronutrients of stomach contents, we first determined dry matter (DM) by drying a subsample of 10 gram in a drying oven (Mettler UM600, Schwabach, Germany) at 100°C for 24h. Another subsample was used for wet sieve analysis with a Retsch VS1000 laboratory sieve analyser (Retsch GmbH, Haan, Germany) with mesh sizes of 16, 8, 4, 2, 1, 0.5, 0.25, 0.125 and 0.063mm (sieves from Retsch GmbH, Haan, Germany). Particles of each fraction were transferred onto pre-weighed Petri dishes, dried at 100°C for 24 h in the drying oven (Mettler UM600, Schwabach, Germany), and weighed after cooling to room temperature in an exsiccator. For the comparison of the proportion of particles passing the finest sieve, the modulus of fineness (MOF) was calculated for each sample (Poppi *et al.* 1980; Clauss, Lechner-Doll & Streich 2002).

The energy [KJ per g dry matter] of each sample was determined by burning in a bomb calorimeter (C5000 IKA Labortechnik, Staufen, Germany). The acid-insoluble ash (AIA, [%]) was determined from acid treated raw ash which was produced in a muffle furnace (Heraeus Instruments, Bremen, Germany). Nitrogen concentration was measured with an N-analyser (Elementar rapid NIII, Langenselbold, Germany); the protein content [%] of a sample was calculated from the nitrogen concentration by multiplication with 6.25. A fibre analyser (Ankam200, New York, USA) was used for fibre analysis [%]. Starch [%] was determined using a laboratory kit (Boehringer, Mannheim, Germany) and a photometer (Tecan sunrise, Crailsheim, Germany). Crude fat [%] was determined with a fat analyser (Gerhardt Soxhmer, Königswinter, Germany). A detailed method description can be found in Schwarm *et al.* (2006).

DATA ANALYSES

Analysis of landscape variables

Based on results of population genetic analyses we further separated the urban forest-WB into two groups (Stillfried *et al.* 2016), resulting in the following classification (rural-WB)

“Brandenburg” included all WB sampled within Brandenburg or Pankow; (city-WB) “Berlin”, included all samples which were collected within non-forest areas of Berlin; (urban forest-WB) with subunits of “Grünwald” containing all samples from the Grünwald forest and “Köpenick” contained all samples from the Köpenick forest (Fig. 4.1).

Sample locations for each stomach were imported into QGIS (version 2.14.1, QGIS-Development-Team, Essen, Germany) and a buffer of 2 km² area was calculated around each location (Fig. 4.1). The size of the buffer was based on average home range sizes of GPS-tracked WB within the urban part of the study area (Stillfried et al. in prep.). The percentage of different habitat types (greenland, agriculture, deciduous and coniferous forest and houses) was calculated for each buffer using a habitat map (classification information see Chapter 3). Additionally, a human population density map (StatIS-BBB 2014) was used to calculate mean human density per km² for each buffer. The percentage of sealed surface was calculated for each buffer by using the extract function in the statistical software R (version 3.3.1, R-Core-Team 2015) using a 100x100m raster (Copernicus 2012).

STATISTICAL ANALYSES

Macroscopic analysis

For the macroscopic analysis, we counted and displayed every single anthropogenic food item (due to the small amount of anthropogenic food sources, statistical analyses were omitted). To test the distribution of stomach categories within different genetic clusters, we used a χ^2 -test and plotted the results in a mosaic plot. The colours used for the groups are the same as used in Fig. 4.1.

Landscape within groups of different origin

The distribution of human related landscape variables (sealed surface, houses and human density detailed variable description in Tab.4.1), forest related landscape variables (deciduous and coniferous) and green areas (greenland and agriculture) within the categories were tested with linear mixed models (LMMs, MuMin package, Barton 2011). Models including each of the previously listed variables as response, the categories as fixed effect and month and forest area as crossed random factors (“Origin-model”) were compared with the corresponding null model. We used log-likelihood ratio tests and information criteria (Akaike Information

criterion corrected for small sample sizes, AICc and Bayesian Information Criterion, BIC) to check whether the final model was superior to an intercept-only or a reduced model. Models were considered similar if differences in AICc were less than 2.5 (Hilbe 2009); as the evaluation of our models with all information criteria produced similar conclusions, we further discussed only AICc values. Significance of each level - within the predictor variable 'category' - was determined by the Tukey post-hoc test (function glht in R library multcomp, Hothorn, Bretz & Westfall 2008).

Macronutrients within origin and stomach categories

In a second model set, we used LMMs (family = gaussian) to test either energy, MOF, AIA, protein, starch, fat or fibre as response variable and the origin category and stomach content category as explanatory variables (= "Origin-StomCat-model"). Model configuration, selection and determination of significant differences of levels within origin- and stomach-content-category were conducted as described above.

Tab. 4.1: Overview of variables which were used for linear mixed models, analysing wild boar stomach contents from animals sampled in Berlin and Brandenburg between 2012 and 2015. A first set of models was testing the variation of landscape variables within different spatial areas. In a second model set, nutrient values and how they vary among groups of genetic origin, among different stomach content categories and in relation to landscape variables, were tested.

Name	Description
Origin	SPATIAL VARIABLE: origin of wild boar: <ul style="list-style-type: none"> • Brandenburg (BB) - rural group • Grunewald (GW) -1st urban forest • Koepenick (KO) -2nd urban forest • Berlin city (BE) - wild boar from built up areas of Berlin
Stomach Category (SC)	MACROSCOPIC VARIABLE: regarding the most dominant contents: <ul style="list-style-type: none"> • Acorn – including only Acorn and grubs • Acorn /Fiber – Mix of different fiber types and acorn • Fiber – only fiber • Maize – mostly maize, but mixed with several other contents • Mix – when none of the above groups fitted
Sealing Houses	% of sealed surface within each wild boar area-human associated variable
Human Density	% of buildings + house with garden -human associated variable
Deciduous	Mean human density (HumDens) per km ² -human associated variable
Coniferous	% of deciduous forests within each wild boar area- forest variable
Greenland	% of coniferous forests within each wild boar area- forest variable
Agriculture	% of public and private greenlands – greenland variable
Month	% of agricultural area – greenland variable
Forest area	Temporal random factor: month when sample was collected.
	Spatial random factor: forest area where the sample was collected.

Impacts of landscape variables on macronutrients

In a third set of models, the above mentioned landscape variables were used as fixed effects, using Energy, MOF, AIA, amount of Protein, Starch, Fat and Fibre as response (LMM with family = gaussian; Tab. 4.1). We compared a set of candidate models (Tab. S 6.4.2) for each response variable, whereas a “LS” included all landscape variables, the models “Hum1”-“Hum4” contained only human related landscape variables, the “For1”-“For3” models contained only forest variables and the “agr1”-“agr3” models contained only greenland and agriculture or the single variables (List of candidate models in Tab. S 6.4.2). The “null” model contained only the random factors. Prior to LMM fitting we tested the explanatory variables for correlation, and only variables with < 0.7 were retained (Fig. S 6.4.2). Homoscedasticity and residual normality of all fitted models were visually assessed with diagnostic plots. Due to multicollinearity of landscape variables in the different origin categories, for the response variable energy, we split this analysis and ran a separate model set for each origin. There was no residual multicollinearity within used models (calculated with the function `vif.mer`, adapted from `rms::vif`, downloaded from <https://raw.githubusercontent.com/aufrank/R-hacks/master/mer-utils.R>). No multicollinearity was present among variables used in the set of models, but single variables had to be removed for the within-origin analysis (for the response energy, agriculture was not present in the Grunewald and Koepenick forest and was therefore not used, deciduous forest was removed from the model sets for Brandenburg and Berlin).

Results:**MACROSCOPIC ANALYSIS: ANTHROPOGENIC FOOD ITEMS AND STOMACH CONTENT CATEGORIES**

16 out of 265 of the WB stomachs used for the macroscopic analysis contained potential anthropogenic food (Tab. S 6.4.1). Five stomachs contained apples. Apple containing stomachs were collected in BB (3), BE (1), and KO (1) between December and February. Four WB from BE consumed bread and two of them did not only contain bread, but also cucumber, salami and cheese. In five stomachs (2.26%) we found pieces of plastic. Two of these stomachs were collected in BE, two in GW and one in KO.

All other stomachs contained only natural food and were assigned to one of the following categories: The “acorn-fibre-stomach” consisted of mostly acorn and different types of fibre

with different quantitative compositions. The “acorn-stomach” contained mostly acorn, often mixed with cockchafer grubs, but no fibre. The “fibre-stomach” contained mostly fibres, roots and reed. The “maize-stomach” contained a high amount of maize, often mixed with acorn but no fibres. All stomachs that did not fit into one of the described category were labelled as “mix-stomach”.

STOMACH CONTENT CATEGORIES VS. ORIGIN CATEGORY

We found a significant difference for the distribution of stomach content categories among the different regions of sampling (Pearson's Chi-squared test, $X^2 = 33.64$, $df = 12$, $P = 0.00076$, $\Phi = 0.37$, $n = 248$). While all five stomach categories were found in BB and BE and GW, there were no Acorn stomachs in the KO group (Fig. 4.2). The acorn-fibre-stomach was most dominant in BB, BE and GW, whereas the fibre-stomach was most common in KO (Fig. 4.2).

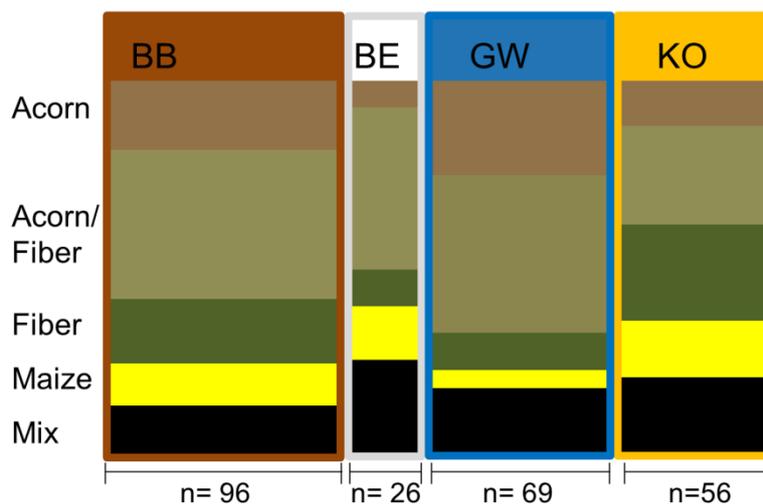


Fig. 4.2: Distribution of wild boar stomach categories among groups of different origin from Berlin and Brandenburg between 2012 and 2015. Different origins were rural Brandenburg (brown box, BB), the urban forests Grunewald (blue box, GW) and Koenpenick (yellow box, KO) and the city of Berlin (white box, BE). Wild boar stomachs were assigned to the stomach categories “Acorn (dark brown), Fibre (olive green), Fibre (green), Maize (yellow), Mix (black)“, due to most dominant content, related to a macroscopic stomach content analysis. Results of Pearson’s Chi-squared test: X -squared = 24.397, $df = 12$, p -value = 0.0179.

LANDSCAPE WITHIN GROUPS OF DIFFERENT ORIGIN

Model selection revealed that all tested landscape variables differed among the origins, as the model including origin as fixed effect was the best model in all model sets (Tab. S 6.4.1). But

the posthoc test revealed significance among levels only for the following landscape variables (Fig. S 6.4.2A):

Percentage of houses was highest in the city origin (38%) and in the urban Koepenick forest (35%) and lowest in the urban forest Grunewald (10%, Fig. 4.3). Percentage of deciduous forest is significantly higher in the urban forest (GW, 75%) and lowest in Brandenburg (BB) (23%).

BB has also a high percentage of greenland (18%, significantly different to Grunewald and Koepenick) and a high percentage of agriculture (30%), which is significantly lower (between 5 and 10%) in BE, GW and KO (Fig. 4.4, Fig. S 6.4.2A).

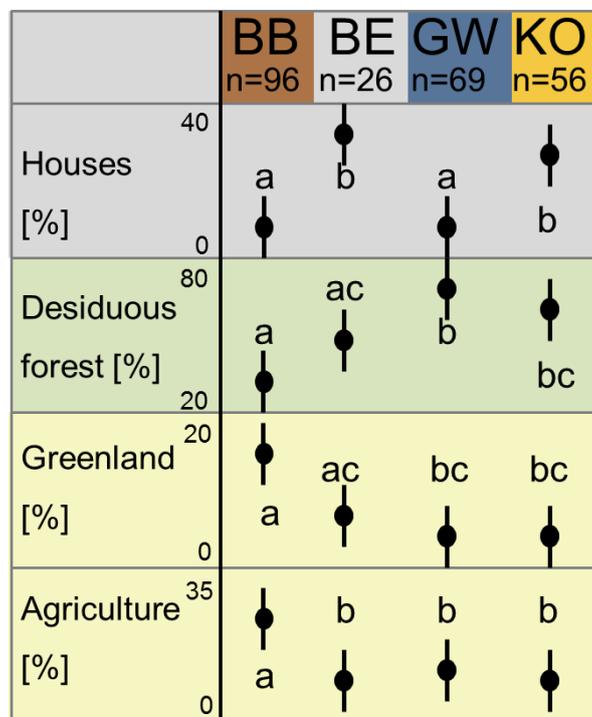


Fig. 4.3: Variation of different landscape variables within groups of different origin in wild boar from Berlin and Brandenburg between 2012 and 2015. Different origin levels were rural Brandenburg (brown box, BB), the urban forests Grunewald (blue box, GW) and Koepenick (yellow box, KO) and the city of Berlin (grey box, BE). Landscape variables are either human associated landscape variables (grey shade) such as percentage of sealed area, percentage of houses or human density within a buffer per km², forest associated landscape variables (green shade) include percentage of deciduous forest and percentage of coniferous forest or greenland associated variables (yellow) are percentage of greenland and agriculture. Significance of each origin level- within the predictor variable origin was determined by the Tukey post hoc test. Significance of the levels of each origin category is visualized by numbers (a-c). Significance between two origins is given when the letters are different. Horizontal lines show the standard error of levels.

MACRONUTRIENTS WITHIN ORIGIN AND STOMACH CATEGORIES

All variables except the MOF varied among genetic cluster and stomach content categories. For all candidate model sets, the best model was the “Origin-StomCat-model, but significant differences among levels of origin were only observed for Energy (Tab. S 6.4.2).

The Energy amount was significantly higher in the urban forest group 1 (22KJ/g, Fig. S 6.4.2B) than in rural areas. The food items within acorn-stomachs (21.5KJ/g) contained significantly more energy than fibre and acorn-fibre-stomachs but similar amounts to maize stomachs. AIA values were lowest in acorn (4%) and maize (4%) stomach and highest within fibre-stomachs (12%, Fig. 4.3, Fig. S 6.4.2B). Protein was highest within the fibre-stomach (25%) whereas the maize stomach showed the lowest protein value (15%). The percentage of Starch within maize-stomachs was highest with 40% and lowest within fibre stomachs (10%). Acorn stomachs contained 14% Fat, while other stomach categories had about 10% fat. The percentage of Fibre is also highest within fibre stomachs (11% Fig. 4.3, Fig. S 6.4.2B).

IMPACTS OF LANDSCAPE VARIABLES ON MACRONUTRIENTS

The model selection resulted in several models with an AICc below 2.5 considered as equally well fit. The null-model was the model with the lowest AICc or had a delta AICc below 2.5 for most of the response variables (Tab. 4.2) indicating a low impact of the landscape on macronutrient. Nevertheless, Energy, AIA, Protein and Starch correlated with single landscape variables which are described and displayed more detailed (Fig. 4.4):

Energy content decreased with increasing percentage of agriculture within the city group. In the Grunewald forest, the amount of energy decreased with increasing percentage of deciduous forest and in Brandenburg, the amount of energy increased with increasing percentage of soil sealing (Fig. 4.4). Agriculture was negatively associated with AIA (values decreasing from 10 to 6% with increasing percentage of agriculture) and positively with starch (values increasing from 15 to 35% with increasing percentage of agriculture). The percentage of Starch decreased from 30 to 12% with increasing percentage of greenland and agriculture from 12 to 35%. An increasing percentage of coniferous forests resulted on the in a decrease of the percentage of Protein (from 22 to 17%).

A:					B:											
Origin				Stomach Category					RESPONSE	Greenland	Agriculture	Deciduous	Coniferous	Houses	Sealing	HuDens
BB	BE	GW	KO	Acorn	Acorn/ Fiber	Fiber	Maize	Mix		% area	% area	% area	% area	% area	% area	People/ km ²
a	ab	b	ab	a	b	b	ab	b	Energy ²² [KJ/g Dry matter] 18		Only Berlin	Only Grunewald			Only Brandenburg	
				a	ab	b	a	ab	AIA [%] 12							
				ac	a	bd	a	cd	Protein [%] 25							
				a	ab	c	d	abe	Starch [%] 40							
				a	ab	b	b	b	Fat [%] 15							
				ac	a		c	a	Fiber [%] 12							
						b			4							

Fig. 4.4: Variation of macronutrients of wild boar from Berlin and Brandenburg between 2012 and 2015; Separate sets of models were run (A) among groups of different origin and within stomach content categories and (B) in relation to different landscape structures.

The energy amount of each stomach content was measured in KJ/g dry matter, the acid insoluble ash (AIA) is given in percent dry matter, such as amount of protein, starch, fat and fibre. Different origins were rural Brandenburg (brown box, BB), the urban forests Grunewald (blue box, GW) and Koepenick (yellow box, KO) and the city of Berlin (white box, BE). Wild boar stomachs were assigned to one of the stomach categories “Acorn (dark brown), Acorn/Fibre (olive green), Fibre (green), Maize (yellow), Mix (black)“, due to most dominant content, related to a macroscopic stomach content analysis. Significance of each level-within the predictor variable cluster and stomach category was determined by the Turkey post hoc test ($\alpha < 0.05$). Significant differences of levels of each category were visualized by labeling with characters a-e. Model selection Table: Tab. S 6.4.4.

Because the previous analysis (A) revealed differences only for the amount of Energy within different clusters, we run a separate model for each clusters. The landscape variables around each sample location and were grouped regarding their expected influence: Sealing (percentage of sealed surface), houses (percentage of houses) and HumDens (Human density per km²) are human associated landscape variables and shaded in grey. Deciduous (percentage of deciduous forest and Coniferous (percentage of coniferous forest) are forest associated landscape variables (shaded in green).Greenland (percentage of greenland) and Agriculture (percentage of agriculture) are field associated landscape variables (shaded in yellow). The continuous lines show the effects of the landscape, the dashed lines indicate the 95% confidence intervals. Associated model selection Table: Tab. 4.2, Tab. S 6.4.5.

Tab. 4.2: Model selection Tab. for linear mixed models, testing nutrient values and food quality in stomachs of wild boar from Berlin and Brandenburg between 2012 and 2015. For different response variables, the energy amount of each stomach (EneBB= Energy within stomachs of wild boar from Brandenburg, EneBE= from Berlin city, EneGW= from the urban Grunewald forest, EneKO= from the urbanKoeppenick forest) content was measured in KJ/g dry matter. Because the previous analysis (Fig. 4.5) revealed significant differences only for the amount of Energy within different clusters, we run a separate model for each cluster. (Because of multicollinearity between the origins and the landscape variable, it was not possible to use cluster as an interaction term in the model, therefore we split the analysis). The modulus of fines (MOF) was calculated after particle size determination; the acid insoluble ash (AIA) is given in percent, such as amount of protein, starch, fat and fibre.

The explanatory variables describe the landscape within a buffer around each sample location: Sealing (percentage of sealed surface), houses (percentage of houses) and HumDens (Human density per km²) are human associated landscape variables, shaded in grey. The Models, which include only these variables, are called “Hum1”-“Hum4”. Deciduous (% of deciduous forest) and Coniferous (% of coniferous forest) are forest associated landscape variables (shaded in green); the models which include only these variables are called “For1”-“For3”. Greenland (% of greenland) and Agriculture (% of agriculture) are field associated landscape variables (shaded in yellow); the model which include only these variables are called “Agr1”-“Agr3”. A model which contains all landscape variables is called “LS”, the intercept only model is called “null”.

The degree of freedom is abbreviated as “df”, the logarithmic likelihood is abbreviated as “logLik”. Akaike’s information criterion corrected for small sample size (AICc) is used for model selection, such as the Bayesian information criterion (BIC). The delta shows the difference between the AICc values. Full model selection table in Tab. S 6.4.4. Detailed variable description in Tab. 4.1.

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Response	Model	Interc.	Sealing	houses	HumDens	Decid-uous	Conif-erous	Green-land	Agricul-ture	df	logLik	AICc	delta	BIC
EneBB	null	19.11								4	-237.15	482.73	0.00	492.55
	Hum2	18.94	0.130							5	-236.35	483.36	0.63	495.51
EneBE	Agr3	19.82							-9.036	5	-55.13	123.26	0.00	126.54
	For1	19.67					1.210			5	-56.23	125.46	2.20	128.75
EneGW	null	20.18								4	-162.22	333.06	0.00	341.37
	For1	22.97				-0.036				5	-161.90	334.76	1.70	344.97
	Hum3	20.13	0.238							5	-162.21	335.38	2.32	345.59
EneKO	null	19.26								4	-120.25	249.29	0.00	256.60
MOF	null	2.96								4	-195.53	399.23	0.00	413.10
	Hum4	2.89		0.009						5	-198.14	406.52	7.29	423.82
AIA	null	8.23								4	-853.87	1715.91	0.00	1729.78
	Agr3	8.82							-0.113	5	-853.96	1718.17	2.25	1735.46
Protein	For3	18.81					-0.062			5	-751.45	1513.14	0.00	1530.43
	null	17.50								4	-752.73	1513.62	0.48	1527.49
Starch	Agr3	23.51							0.206	5	-998.37	2007.00	0.00	2024.29
	null	24.06								4	-999.73	2007.63	0.64	2021.50
	For3	21.05					0.133			5	-999.07	2008.38	1.39	2025.68
	Agr1	24.26						-0.120	0.205	6	-998.19	2008.73	1.73	2029.43
	Agr2	24.85						-0.127		5	-999.41	2009.07	2.07	2026.34
Fat	null	8.73								4	-851.90	1711.97	0.00	1725.84
Fibre	null	9.34								4	-750.38	1508.93	0.00	1522.80

Discussion

ANTHROPOGENIC FOOD SOURCES

Almost no anthropogenic food items were found in WB stomachs. Thus, the general assumption that WB enter cities to primarily consume human garbage or receive direct feeding needs to be reconsidered. Moreover, groups of different origin might differ in resource availability due to the local landscape.

Contrasting to our findings, WB from Barcelona or Islamabad frequently consume anthropogenic food (Hafeez *et al.* 2011; Cahill *et al.* 2012). Even if our study underestimated the amount of anthropogenic food as some food items get digested more rapidly (Putman 1984; Schley & Roper 2003) or some plant fibres might origin from human composts and were not identifiable as human-associated, WB consumed mostly natural food.

Comparable omnivores such as black bears foraged extensively in urban areas when natural food production was poor, but switched to natural food sources whenever available (Lewis *et al.* 2015). However, black bears in Montana foraged on human foods near houses even when natural foods were available (Merkle *et al.* 2013). Coyotes in Chicago consumed human-associated food during pup-rearing and dispersal seasons, i.e. when energy demands are high (Morey, Gese & Gehrt 2007). Most of our WB stomach samples were collected during late-autumn/winter, when the fat-content of natural food was higher than in summer due to mast production of acorn. Damage of WB on public and private properties was mostly observed during summer (personal observation). Since WB switch diets seasonally (Briedermann 1976; Massei, Genov & Staines 1996; Schley & Roper 2003) our results show a typical winter pattern.

It might be possible that the local WB preferred natural food sources by choice. Another possibility might be that human associated food sources were difficult to access by WB in our study region, as the Berlin senate campaigned to inform people that supplementary feeding wildlife is illegal (detailed information and Flyer on the homepage of Berlin: http://www.stadtentwicklung.berlin.de/forsten/wildtiere/download/fuettern_nein_danke.pdf). and the Berlin forestry departments removed all garbage bins from the forests to reduce the amount of garbage left by people (Franusch 2000; Franusch 2014). In Colorado, bear-resistant garbage containers existed, but more than 50% were not properly secured (Lewis *et al.* 2015). Baboons (*Papio ursinus*) in South Africa showed a strong preference for anthropogenic food,

thus fencing of waste sites resulted in a decreased appearance of baboons in urban areas (Kaplan *et al.* 2011). We infer limited accessibility of human garbage is a viable management tool and combined with further public education even more effective in preventing wildlife conflicts, as highly flexible omnivores are known to switch diets in relation to food availability (Briedermann 1976; Massei, Genov & Staines 1996; Schley & Roper 2003).

STOMACH CONTENT CATEGORIES AND ORIGIN

The five stomach content categories found in WB of our study area were comparable with major herbal food categories reported for WB (Schley & Roper 2003) consuming mostly plant material (Massei, Genov & Staines 1996; Hafeez *et al.* 2012; Cuevas *et al.* 2013; Ballari & Barrios-Garcia 2014; Merta *et al.* 2014). However, the omnivorous WB (Herrero *et al.* 2006) feeds various foods, but is selective for high forage quality and high carbohydrate contents (Cuevas *et al.* 2013). Beside specific behavioural patterns, WB diet is a result of environmental characteristics and resources (Herrero *et al.* 2006). WB from the GW had the highest percentage of acorn stomachs. Acorns contain a high amount of fat (Gea-Izquierdo, Cañellas & Montero 2006). The relatively high percentage of protein (20%) in acorn-stomachs, despite acorn containing low amounts of protein (Gea-Izquierdo, Cañellas & Montero 2006), fits to our observations that acorn was often consumed together with a large number of cockchafer grubs providing the necessary protein (Laznik & Trdan 2014). Altogether we infer food quality and available energy are higher in the GW forest than in the KO forest, which coincides with a reduced acorn availability in the KO forest.

Numerous studies describe that WB forage within agricultural areas and are crop pests (Schley & Roper 2003; Herrero *et al.* 2006; Keuling, Stier & Roth 2009; Amici *et al.* 2012; Hafeez *et al.* 2012; Frackowiak *et al.* 2013; Ficetola *et al.* 2014; Nasiadka & Janiszewski 2015). Maize is often consumed (Herrero *et al.* 2006) and is known for its high amount of carbohydrates, supporting our finding that the amount of starch increases with increasing percentage of agricultural area and is the highest in maize-stomachs (40%). Interestingly, we found high amount of maize-stomachs in KO forest and the City group, although there were relatively few agricultural areas. We assume, that most of the maize consumed in KO and BE (including forest edges of KO and GW) is a result of anthropogenic supplemental food (Cellina 2008; Ballari *et al.* 2015). Maize as hunting bait is frequently used during hide hunts

and many samples from BE and KO originate from those, whereas most of the samples from GW and BE originate from battue hunts where no baiting is used.

FORAGE QUALITY AND RISK AVOIDANCE

An optimal access to food, as described by optimal foraging theory depends on the type of food choice, optimal patch choice and time management (Emlen 1966; MacArthur & Pianka 1966; Charnov 1976; Pyke, Pulliam & Charnov 1977; Krebs 1978; Pyke 1984). Our results showed that the type of food choice and the quality differed among groups of different origin. A high MOF value indicates high fibre content and therefore poor quality because fibre provides little energy and is difficult to digest (Noblet & Perez 1993; Wenk 2001). Our analyses revealed no impact of MOF and fibre content within cluster and stomach category or in relation with different landscape variables. Therefore, we assume that MOF is a poor predictor for the quality of WB nutrition. Acid insoluble ash (AIA) indicates the amount of indigestible soil which is unintentionally ingested by feeding wildlife (Beyer, Connor & Gerould 1994). Rooting WB might ingest more soil, hence, we considered the amount of AIA as an indicator of rooting intensity within a landscape. AIA is negatively associated with the percentage of agriculture, thus rooting does not play a role in agricultural areas. There was no correlation between AIA and greenland which might be a result of the sampling season, because rooting damages in the city occur mostly in summer (personal observation). AIA is increased in fibre-stomachs, which are abundant in the urban Koepenick forest, indicating increased rooting activity in this area.

Regarding the optimal patch choice (MacArthur & Pianka 1966; Charnov 1976; Pyke, Pulliam & Charnov 1977), our results showed that landscapes differ within different origins, indicating that different areas provide different food. A study about habitat selection in urban and rural WB from the same study region (Stillfried et al. in prep.) shows, that urban WB modulate a landscape of fear by spatial and temporal adjustment (e.g. patch choice and time management), i.e. they strongly avoided humans during the day, but foraged close to houses during the night. Based on these findings and our results presented here, we infer that WB which invade cities have to adjust their general spatial and temporal behaviour to avoid predation and to forage natural resources within urban areas.

CONCLUSION

Landscape variables such as lower percentages of forest, agriculture and greenland were associated with macronutrients, while human associated landscape variables had a low impact on quality of WB nutrition. Even areas showing high percentages of sealed surface and houses contain greenland and trees providing natural food which is easily accessible for omnivorous urban utilizers such as WB. Anthropogenic food such as garbage might serve as fallback food when access to natural resources is limited. Finally, we infer that WB became tolerant to disturbance by human urbanites and forage abundant, natural resources within urban areas. Moreover, free ranging WB might only use anthropogenic resources easily to exploit and more abundant than natural resources – a characteristic behaviour of omnivores.

Acknowledgements

We would like to thank Heidrun Barleben, Linda Bistere and Tim Bornholdt for laboratory analyses. We thank the Berlin and Brandenburg forestry departments for providing samples. Many thanks also to “Stiftung Naturschutz Berlin” and National Geographic and the Leibniz Institute for Zoo and Wildlife Research for funding the WB project. PG was funded by the German Federal Ministry of Education and Research BMBF within the Collaborative Project "Bridging in Biodiversity Science - BIBS" (funding number 01LC1501A-H)

References

- Amici, A., Serrani, F., Rossi, C.M. & Primi, R. (2012) Increase in crop damage caused by wild boar (*Sus scrofa* L.): the "refuge effect". *Agronomy for Sustainable Development*, **32**, 683-692.
- Ballari, S.A. & Barrios-Garcia, M.N. (2014) A review of wild boar *Sus scrofa* diet and factors affecting food selection in native and introduced ranges. *Mammal Review*, **44**, 124-134.
- Ballari, S.A., Cuevas, M.F., Ojeda, R.A. & Navarro, J.L. (2015) Diet of wild boar (*Sus scrofa*) in a protected area of Argentina: the importance of baiting. *Mammal Research*, **60**, 81-87.
- Barton, K. (2011) MuMIn: Multi-model inference. R package version 1.0. 0. Vienna, Austria: R Foundation for Statistical Computing. See <http://CRAN.R-project.org/package=MuMIn>.
- Beninde, J., Veith, M. & Hochkirch, A. (2015) Biodiversity in cities needs space: a meta-analysis of factors determining intra-urban biodiversity variation. *Ecology Letters*, **18**, 581-592.
- Berlin, S.f.S.u.U. (2015) Alters und Bestandsstruktur der Wälder www.stadtentwicklung.berlin.de/umwelt/umweltatlas/e_text/kb504.doc.
- Beyer, W.N., Connor, E.E. & Gerould, S. (1994) Estimates of soil ingestion by wildlife. *The Journal of Wildlife Management*, **58**, 375-382.

- Bonnot, N., Morellet, N., Verheyden, H., Cargnelutti, B., Lourtet, B., Klein, F. & Hewison, A.J.M. (2013) Habitat use under predation risk: hunting, roads and human dwellings influence the spatial behaviour of roe deer. *European Journal of Wildlife Research*, **59**, 185-193.
- Börner, K. & Olbertz, J.-H. (2014) *Untersuchungen zur Raumnutzung des Rotfuchses, Vulpes vulpes (L., 1758), in verschiedenen anthropogen beeinflussten Lebensräumen Berlins und Brandenburgs*. mbv, Mensch-und-Buch-Verlag.
- Briedermann, L. (1976) Ergebnisse einer Inhaltsanalyse von 665 Wildschweinemägen. *Zoologischer Garten, Neue Folge, Jena*, 157-185.
- Brown, J.S., Laundre, J.W. & Gurung, M. (1999) The ecology of fear: Optimal foraging, game theory, and trophic interactions. *Journal of Mammalogy*, **80**, 385-399.
- Bueno, C.G., Alados, C.L., Gómez-García, D., Barrio, I.C. & García-González, R. (2009) Understanding the main factors in the extent and distribution of wild boar rooting on alpine grasslands. *Journal of Zoology*, **279**, 195-202.
- Cahill, S., Llimona, F., Cabaneros, L. & Calomardo, F. (2012) Characteristics of wild boar (*Sus scrofa*) habituation to urban areas in the Collserola Natural Park (Barcelona) and comparison with other locations. *Animal Biodiversity and Conservation*, **35**, 221-233.
- Cellina, S. (2008) Effects of supplemental feeding on the body condition and reproductive state of wild boar *Sus scrofa* in Luxembourg. *Dissertation, University of Sussex Brighton*.
- Charnov, E.L. (1976) Optimal foraging, the marginal value theorem. *Theoretical Population Biology*, **9**, 129-136.
- Ciuti, S., Northrup, J.M., Muhly, T.B., Simi, S., Musiani, M., Pitt, J.A. & Boyce, M.S. (2012) Effects of Humans on Behaviour of Wildlife Exceed Those of Natural Predators in a Landscape of Fear. *Plos One*, **7**, 13.
- Clauss, M., Lechner-Doll, M. & Streich, J.W. (2002) Faecal particle size distribution in captive wild ruminants: an approach to the browser/grazer dichotomy from the other end. *Oecologia*, **131**, 343-349.
- 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.
- Copernicus (2012) High Resolution Layer: Imperviousness Degree (IMD) Copernicus Land Monitoring Services - European Environment Agency (EEA). with funding by the European Union.
- Cuevas, M.F., Ojeda, R.A., Dacar, M.A. & Jaksic, F.M. (2013) Seasonal variation in feeding habits and diet selection by wild boars in a semi-arid environment of Argentina. *Acta Theriologica*, **58**, 63-72.
- Emlen, J.M. (1966) The role of time and energy in food preference. *American Naturalist*, 611-617.
- Ficetola, G.F., Bonardi, A., Mairota, P., Leronna, V. & Padoa-Schioppa, E. (2014) Predicting wild boar damages to croplands in a mosaic of agricultural and natural areas. *Current Zoology*, **60**, 170-179.
- Fischer, J.D., Schneider, S.C., Ahlers, A.A. & Miller, J.R. (2015) Categorizing wildlife responses to urbanization and conservation implications of terminology. *Conservation Biology*, **29**, 1246-1248.
- Frackowiak, W., Gorczyca, S., Merta, D. & Wojciuch-Ploskonka, M. (2013) Factors affecting the level of damage by wild boar in farmland in north-eastern Poland. *Pest Management Science*, **69**, 362-366.
- Franusch, M. (2000) "Erholungsmüll": Aktion sauberer Wald: Alle Papierkörbe weg. Der Tagesspiegel, article by Ingo Bach, 15.11.2000.
- Franusch, M. (2014) "Waldgebiet des Jahres 2015" Berlin_Grunewald. Grunewald, ein Wald für alle, Berliner Zeitung, article by Anne Lena Mösken, 28.11.2014.
- Frid, A. & Dill, L. (2002) Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology*, **6** (1): 11.
- Gea-Izquierdo, G., Cañellas, I. & Montero, G. (2006) Acorn production in Spanish holm oak woodlands. *Forest Systems*, **15**, 339-354.

- Hafeez, S., Abbas, M., Khan, Z.H. & Rehman, E.U. (2011) Preliminary analysis of the diet of wild boar (*Sus scrofa* L., 1758) in Islamabad, Pakistan. *Turkish Journal of Zoology*, **35**, 115-118.
- Hafeez, S., Ashfaq, M., Hafeez, T., Ahsan, M. & Tiwana, U. (2012) Preliminary analysis of the diet of wild boar (*Sus scrofa* L., 1758) in an agroecosystem of central Punjab, Pakistan. *Turkish Journal of Zoology*, **36**, 676-681.
- Herrero, J., García-Serrano, A., Couto, S., Ortuño, V.M. & García-González, R. (2006) Diet of wild boar *Sus scrofa* L. and crop damage in an intensive agroecosystem. *European Journal of Wildlife Research*, **52**, 245-250.
- Herrero, J., Irizar, I., Laskurain, N.A., García-Serrano, A. & García-González, R. (2005) Fruits and roots: wild boar foods during the cold season in the southwestern Pyrenees. *Italian Journal of Zoology*, **72**, 49-52.
- Hothorn, T., Bretz, F. & Westfall, P. (2008) Simultaneous inference in general parametric models. *Biometrical journal*, **50**, 346-363.
- Kaplan, B.S., O'Riain, M.J., van Eeden, R. & King, A.J. (2011) A Low-Cost Manipulation of Food Resources Reduces Spatial Overlap Between Baboons (*Papio ursinus*) and Humans in Conflict. *International Journal of Primatology*, **32**, 1397-1412.
- Keuling, O., Stier, N. & Roth, M. (2009) Commuting, shifting or remaining? Different spatial utilisation patterns of wild boar *Sus scrofa* L. in forest and field crops during summer. *Mammalian Biology*, **74**, 145-152.
- Kotulski, Y. & König, A. (2008) Conflicts, crises and challenges: wild boar in the Berlin City—a social empirical and statistical survey. *Natura Croatica*, **17**, 233-246.
- Krebs, J.R. (1978) Optimal foraging: decision rules for predators. *Behavioural ecology: An evolutionary approach*, 23-63.
- Laznik, Z. & Trdan, S. (2014) Evaluation of different soil parameters and wild boar (*Sus scrofa* L.) grassland damage. *Italian Journal of Animal Science*, **13**, 759-765..
- Lewis, D.L., Baruch-Mordo, S., Wilson, K.R., Breck, S.W., Mao, J.S. & Broderick, J. (2015) Foraging ecology of black bears in urban environments: guidance for human-bear conflict mitigation. *Ecosphere*, **6**, 1-18.
- Lowry, H., Lill, A. & Wong, B.B.M. (2013) Behavioural responses of wildlife to urban environments. *Biological Reviews*, **88**, 537-549.
- MacArthur, R.H. & Pianka, E.R. (1966) On optimal use of a patchy environment. *American Naturalist*, **100**, 603-609.
- Maibeche, Y., Moali, A., Yahi, N. & Menard, N. (2015) Is Diet Flexibility an Adaptive Life Trait for Relictual and Peri-Urban Populations of the Endangered Primate *Macaca sylvanus*? *Plos One*, **10**, 22.
- Massei, G., Genov, P.V. & Staines, B.W. (1996) Diet, food availability and reproduction of wild boar in a Mediterranean coastal area. *Acta Theriologica*, **41**, 307-320.
- McKinney, M.L. (2002) Urbanization, biodiversity, and conservation. *Bioscience*, **52**, 883-890.
- Merkle, J.A., Robinson, H.S., Krausman, P.R. & Alaback, P. (2013) Food availability and foraging near human developments by black bears. *Journal of Mammalogy*, **94**, 378-385.
- Merta, D., Mocala, P., Pomykacz, M. & Frackowiak, W. (2014) Autumn-winter diet and fat reserves of wild boars (*Sus scrofa*) inhabiting forest and forest-farmland environment in south-western Poland. *Folia Zoologica*, **63**, 95-102.
- Milne, B.T., Turner, M.G., Wiens, J.A. & Johnson, A.R. (1992) Interactions between the fractal geometry of landscapes and allometric herbivory. *Theoretical Population Biology*, **41**, 337-353.
- Morey, P.S., Gese, E.M. & Gehrt, S. (2007) Spatial and temporal variation in the diet of coyotes in the Chicago metropolitan area. *American Midland Naturalist*, **158**, 147-161.
- Murray, M., Cembrowski, A., Latham, A.D.M., Lukasik, V.M., Pruss, S. & St Clair, C.C. (2015) Greater consumption of protein-poor anthropogenic food by urban relative to rural coyotes increases diet breadth and potential for human-wildlife conflict. *Ecography*, **38**, 1235-1242.
- Nasiadka, P. & Janiszewski, P. (2015) Food preferences of wild boars (*Sus scrofa* L.) in the summer and early autumn expressed by the damage caused in agricultural crops. *Sylvan*, **159**, 307-317.

- Noblet, J. & Perez, J. (1993) Prediction of digestibility of nutrients and energy values of pig diets from chemical analysis. *Journal of animal science*, **71**, 3389-3398.
- Nowak, D.J., Noble, M.H., Sisinni, S.M. & Dwyer, J.F. (2001) People and trees: assessing the US urban forest resource. *Journal of Forestry*, **99**, 37-42.
- Otoni, I., de Oliveira, F.F.R. & Young, R.J. (2009) Estimating the diet of urban birds: The problems of anthropogenic food and food digestibility. *Applied Animal Behaviour Science*, **117**, 42-46.
- Pauleit, S., Jones, N., Garcia-Martin, G., Garcia-Valdecantos, J.L., Rivière, L.M., Vidal-Beaudet, L., Bodson, M. & Randrup, T.B. (2002) Tree establishment practice in towns and cities—Results from a European survey. *Urban Forestry & Urban Greening*, **1**, 83-96.
- Pierce, G.J. & Ollason, J.G. (1987) 8 reasons why optimal foraging theory is a complete waste of time. *Oikos*, **49**, 111-118.
- Poppi, D., Norton, B., Minson, D. & Hendricksen, R. (1980) The validity of the critical size theory for particles leaving the rumen. *The Journal of Agricultural Science*, **94**, 275-280.
- Putman, R. (1984) Facts from faeces. *Mammal Review*, **14**, 79-97.
- Pyke, G.H. (1984) Optimal foraging theory: a critical review. *Annual review of ecology and systematics*, **15**, 523-575.
- Pyke, G.H., Pulliam, H.R. & Charnov, E.L. (1977) Optimal foraging: a selective review of theory and tests. *Quarterly Review of Biology*, **52**, 137-154.
- R-Core-Team (2015) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>.
- Rosner, S., Mussard-Forster, E., Lorenc, T. & Muller, J. (2014) Recreation shapes a "landscape of fear" for a threatened forest bird species in Central Europe. *Landscape Ecology*, **29**, 55-66.
- Schley, L. & Roper, T.J. (2003) Diet of wild boar *Sus scrofa* in Western Europe, with particular reference to consumption of agricultural crops. *Mammal Review*, **33**, 43-56.
- Schwarm, A., Ortmann, S., Hofer, H., Streich, W.J., Flach, E.J., Kuhne, R., Hummel, J., Castell, J.C. & Clauss, M. (2006) Digestion studies in captive Hippopotamidae: a group of large ungulates with an unusually low metabolic rate. *Journal of Animal Physiology and Animal Nutrition*, **90**, 300-308.
- Seto, K.C., Fragkias, M., Guneralp, B. & Reilly, M.K. (2011) A Meta-Analysis of Global Urban Land Expansion. *Plos One*, **6**: e23777.
- StatIS-BBB (2014) Einwohnerdichte 2014. *Amt für Statistik Berlin-Brandenburg*, <https://creativecommons.org/licenses/by/3.0/de/>.
- Stillfried, M., Belant, J.L., Svoboda, N.J., Beyer, D.E. & Kramer-Schadt, S. (2015) When top predators become prey: black bears alter movement behaviour in response to hunting pressure. *Behavioural Processes*, **120**, 30-39.
- Stillfried, M., Fickel, J., Börner, K., Wittstatt, U., Heddergott, M., Ortmann, S., Kramer-Schadt, S. & Frantz, A.C. (2016) Do cities represent sources, sinks or isolated islands for urban wild boar population structure? *Journal of Applied Ecology*. DOI: 10.1111/1365-2664.12756.
- Theimer, T.C., Clayton, A.C., Martinez, A., Peterson, D.L. & Bergman, D.L. (2015) Visitation rate and behavior of urban mesocarnivores differs in the presence of two common anthropogenic food sources. *Urban Ecosystems*, **18**, 895-906.
- Tryjanowski, P., Skoraka, P., Sparks, T.H., Biadun, W., Brauze, T., Hetmanski, T., Martyka, R., Indykiewicz, P., Myczko, L., Kunysz, P., Kawa, P., Czyz, S., Czechowski, P., Polakowski, M., Zduniak, P., Jerzak, L., Janiszewski, T., Golawski, A., Dudus, L., Nowakowski, J.J., Wuczynski, A. & Wysocki, D. (2015) Urban and rural habitats differ in number and type of bird feeders and in bird species consuming supplementary food. *Environmental Science and Pollution Research*, **22**, 15097-15103.
- Welander, J. (2000) Spatial and temporal dynamics of wild boar (*Sus scrofa*) rooting in a mosaic landscape. *Journal of Zoology*, **252**, 263-271.
- Wenk, C. (2001) The role of dietary fibre in the digestive physiology of the pig. *Animal Feed Science and Technology*, **90**, 21-33.

CHAPTER 5: General Discussion

5.1. FINDINGS FROM POPULATION GENETICS, HABITAT USE AND NUTRITION

The story of wild boar in Berlin is a story of success. The aim of my thesis was to elaborate the conceptual ecological mechanisms how wild boar adjust to urban environments. Within my study area I defined three groups of wild boar, prior to my analysis (city wild boar, urban forest wild boar and rural wild boar, Fig. 1.2). In **Manuscript 1**, I aimed on investigating if urban areas are sources, sinks or isolated islands. I hypothesized that human dominated urban areas lead to a genetic differentiation between wild boar from Berlin and Brandenburg and that urban wild boar are driven into settlements from overpopulated neighbouring urban forests. My analyses revealed that there are four population clusters: urban forest wild boar are divided into three isolated urban forest populations, with two of Brandenburg population (BB, rural wild boar), while the third urban forest population in Tegel (TE) is a subgroup of the neighbouring Grunewald (Fig. 5.1). City wild boar genetically belong to the Brandenburg population which means that they are rural dispersers which use the city as attractive sink (Fig. 5.1). I further hypothesised in **Manuscript 2** that wild boar in urban environments adjusted their perception of risk, i.e. modulated their landscape of fear, in order to find sufficient forage and shelter in a human dominated environment. I predicted that the trade-off between fear and forage will be biased in favour of forage, if the potential rewards in the urban environment are higher than in the rural one. Therefore, the modulation of the landscape of fear is expected to be stronger than the modulation of the landscape of forage. For this analysis, urban forest wild boar and city wild boar were assigned as novel “urban wild boar” group, which were compared with rural wild boar. I was able to confirm my hypotheses by showing that urban wild boar use habitats which rural conspecifics avoid, such as areas close to bathing sites and roads for resting and areas close to houses for foraging (Fig. 5.1). On the small scale analysis in **Manuscript 3**, I expected to find anthropogenic food sources in urban wild boar and differences in the diet of groups of different origin due to differences in habitat availability. For this part of my study, I analysed rural wild boar from the Brandenburg population as rural (BB) group, I had samples of two of the isolated urban

forest wild boar populations, from the Grunewald (GW) and Koepenick (KO) and as a fourth group is used city wild boar (BE, which belong to the BB-cluster as a separate group). I did not find a significant amount of human food in wild boar stomachs but I found differences in food quality and most dominant food sources within the different origins, with the highest energy found in Grunewald forest (GW, Fig.5.1). Although the landscape differed within the genetic groups, especially human associated landscape variables had as minor effect, only percentage of agriculture, greenland and coniferous forests correlated with some nutrient measurements.

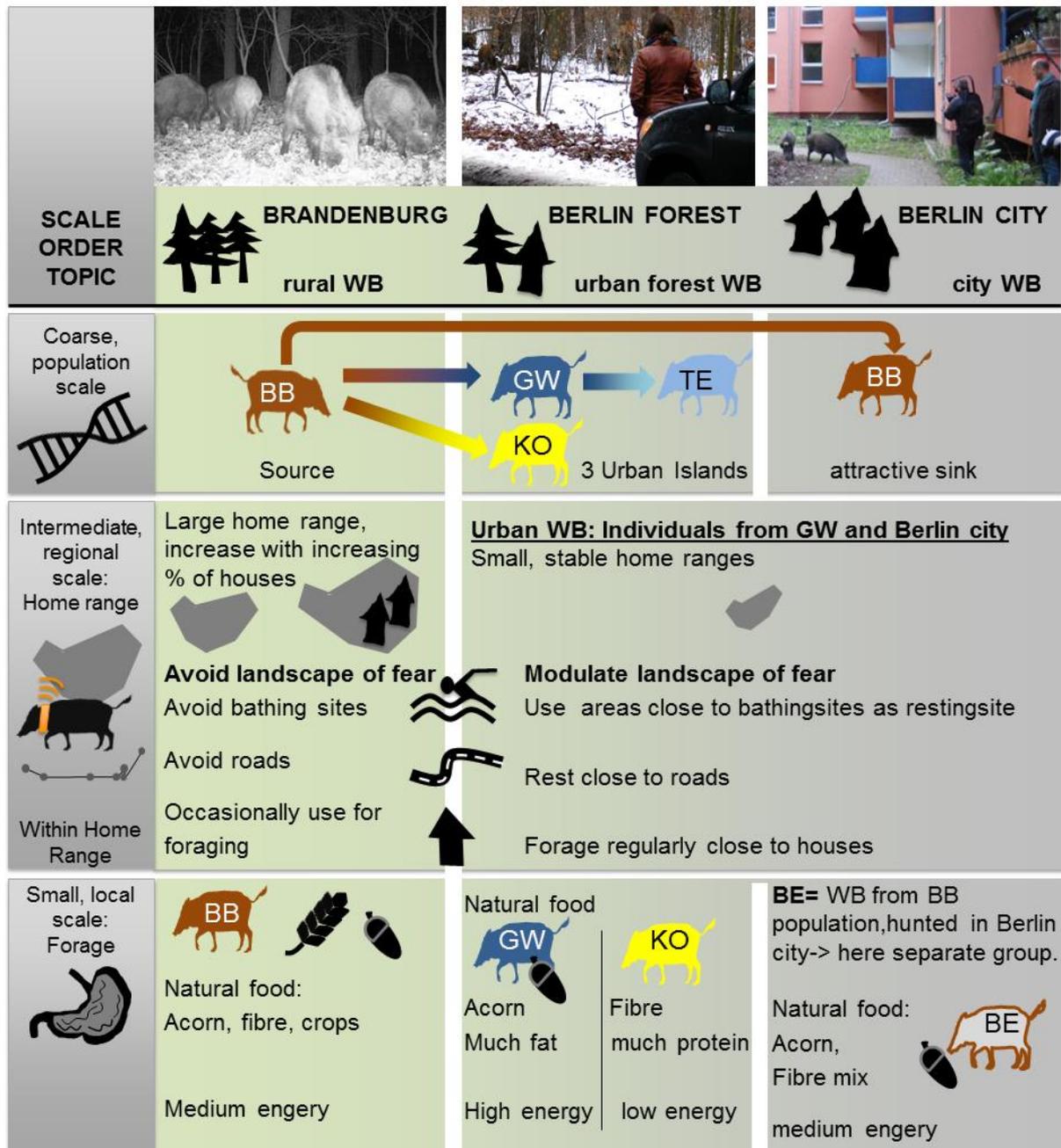


Fig. 5.1: Summary of results for testing ecology of wild boar (WB) in rural and urban environments from coarse to small scale. Three types of wild boar were defined prior to the analysis: Rural WB occur in natural rural environments of Brandenburg, urban forest WB can be easily approached within urban forests, and city WB occur within the urban area of Berlin. Based on the literature, I formulated predictions on a coarse to small scale (Fig. 1.2), the results are displayed in this Fig. in a simplified way. On the coarse scale (population genetic analysis), four different populations were found which are indicated by different colours: Brandenburg (BB, brown, including rural individuals and city wild boar), Grunewald (GW, dark blue) - Koepenick (KO, yellow) and Tegel (TE, light blue) - each including WB from the core area of each urban forest. The arrows show the origin, if the arrow is plain-coloured, there is no genetic differentiation. For the intermediate scale I analysed habitat use for rural wild boar (from Brandenburg) and urban WB which were classified independent from the genetic results, based on characteristics of their home ranges (including individuals from the urban forests and Berlin City). Home ranges of rural WB were taller than those of urban WB and increased with increasing percentage of houses. Within the home range, urban wild boar used human associated landscapes (bathing sites, roads, houses) which were avoided by rural WB. For the small scale analysis, differences in the stomach content in different populations were analysed. Samples from the TE population did not exist and the BB-population was split: BB= all rural individuals, BE (white) = all city wild boar of Berlin. The analyses revealed that even city wild boar consume natural food and no human garbage.

5.2. FROM AVOIDERS, DWELLERS AND UTILIZERS: TYPES OF WILD BOAR IN THE STUDY AREA

Urban avoider populations can be extirpated in developed landscapes but occur in natural areas embedded in an urban matrix (Fischer et al. 2015). Avoidance of habitats can be a result of negative associations as it was observed for Acadian Flycatchers (*Empidonax virescens*) due to lower reproductive success in urban areas (Rodewald & Shustack 2008). Alternatively urban areas can function as perceptual traps as it was observed in Lesser Prairie-Chicken (*Tympanuchus pallidicinctus*). This means, that a high quality habitat is perceived as an ecological trap (= low quality habitat which is selected despite a loss of fitness) and is therefore avoided (Patten & Kelly 2010). In my study rural wild boar from Brandenburg mostly avoid the human associated landscape of fear. But they also show some tolerance to human disturbance when they occasionally forage close to houses when resources in the forest get rare (Manuscript 2; Cluster BB). Rural wild boar form a large population, from which dispersers enter urban built-up areas of Berlin (Manuscript 1). The pre-adjustment and the “urban behaviour” of rural wild boar, which reflects their high learning ability and behavioural flexibility, might be a first step of adjusting to urban areas. They fit therefore only slightly to the definition of urban avoiders and to some extent to the description of urban utilizers, which occasionally use urban resources (Fischer et al. 2015).

Urban forest wild boar were shown to form three isolated populations in the core areas of the urban forest (Manuscript 1, Clusters GW, KO, TE; Fig 5.1) and consume mostly natural food sources (Manuscript 3), which might lead to the conclusion that they are urban avoiders in natural habitats, embedded in the urban matrix of the city of Berlin. Detailed home range and within home range analyses from the core areas of the isolated clusters are only present for one individual (IZW5), the remaining wild boar which were assigned to the “urban” group, were collared and observed at forest edges of the Grunewald which have a significantly lower fleeing distance than rural wild boar and they use landscape-of-fear associated landscape structures such as bathing sites and roads for resting and forage close to houses (Manuscript 2). The nutrient analysis for this type reveals significant differences to the other observed groups but also differences between the urban forest groups, which are related to different habitat availability (Manuscript 3). Therefore they also range from urban avoiders to urban utilizers.

City wild boar are genetically admixed with rural wild boar (Manuscript 1; Cluster BE, Fig. 5.1). Observations of the northern goshawk (*Accipiter gentilis*) were made in parts of the city where territories were established in later years, demonstrating that these early visitors had encountered, but not used, potential nest sites (Rutz 2008). A similar effect might occur in wild boar which can explain why the city group is not genetically isolated but admixed. The colonization of the city is a long-term and dynamic process. But since city wild boar differ significantly from rural wild boar regarding the perception of the landscape of fear (Manuscript 2) fit to the description of urban dwellers which vary from having viable populations in both natural and developed areas (Fischer et al. 2015).

In summary, the concept of urban avoiders, utilizers and dwellers is not optimal to describe the specific characteristics of wild boar in Berlin and Brandenburg, which cover the whole spectrum from avoidance to adjustment. The urban environment seems to be attractive and suitable especially for city wild boar but not for rural wild boar (and urban forest wild boar) which is surprising since city wild boar and rural wild boar belong to the same population. Their high behavioural plasticity (Podgorski *et al.* 2013) enables them to use all available habitats. It is unclear, if city wild boar might be forced to use the city, because other habitats are overpopulated (=city as attractive sink habitat and directly chosen) or if they are driven into urban environments from the source population due to a lack of alternative habitats.

5.3. SOURCES, SINKS AND HABITAT QUALITY

Source habitats are defined as having a high quality with high birth rate and low mortality and lead to a population increase; therefore they might function as source for a low quality sink habitat with low birth rate and high mortality and a population decline (Pulliam 1988; Dias 1996). In order to evaluate the quality of a habitat, different approaches are recommended. Due to van Horne (1983) it is misleading to only use population density, because habitat quality and wildlife density are not necessarily positively correlated. Habitat quality should instead be defined in terms of the survival and production characteristics as well as the density of the species occupying that habitat (Van Horne 1983). Thus, measurements of habitat quality, which only assess use and availability are not adequate, because a mechanistic understanding of relations between resource acquisition by individuals and population dynamics are necessary (Hobbs & Hanley 1990). Non-demographic indicators such as body condition are also of high importance for habitat quality (Johnson 2007). Urban Rufous-collared Sparrows (*Zonotrichia capensis*) have lower body weights and a larger stress index, than rural ones, but after two weeks of captivity rural birds developed blood characteristics that resembled those of urban birds, which indices chronic stress characteristics in the urban birds (Ruiz *et al.* 2002). In summary, numerous ecological factors can lead animals to select poor and avoid rich habitats (Johnson 2007).

Regarding above mentioned recommendations, it is difficult to categorize the different wild boar characters and their habitat types (rural, urban forest and city) as either good quality sink or bad quality source. Manuscript 2 revealed that both availability and use are different in urban and rural habitats. Urban habitats provide fewer natural resources (landscape of food), but therefore more human associated habitats (landscape of fear) are used. The population structure analysis (Manuscript 1) gives the impression that rural habitats function as source, but real population dynamics (relationship between birth rate and mortality) are unknown. A habitat model (Appendix, Fig. S 6.2.1) assessing the breeding capacity for wild boar in Berlin and surrounding Brandenburg based on an algorithm proposed by Fernández, Kramer-Schadt & Thulke (2006) predicted a high breeding capacity per core area for the urban Grunewald (GW) and Tegel (TE) forest and for most parts of Brandenburg (BB) where our samples got collected. The Koepenick (KO) forest has still a high breeding capacity but lower than the two other urban forests. The breeding capacity is lowest in Berlin city (BE). Real mortality rates are unknown, but hunting bag statistics are available which show a high hunting pressure in all areas, including BB, urban forests and even within Berlin due to city hunters (Fig. 2.1).

Hunting pressure might be even stronger in the city due to special financial awards for hunted piglets and because hunters are called if wild boar damage properties (Kopetzki 2016). Detailed measurements of body conditions are missing for the study area, but body weights of hunted juveniles (including all individuals assessed by hunters to be younger than one year) between October and February showed the highest weights of juveniles within Berlin city (BE), followed by wild boar from Brandenburg (BB) and the Grunewald (GW), with the lowest body weights in the Koepenick (KO) forests (Fig. S 6.1.1). These values fit to my own impressions and observations during sample collections, but the data are quite imprecise, because the real age is unknown and wild boar - even if rutting time is mainly in late autumn and early winter (Mauget 1982) - are known to be flexible regarding farrowing time because exogenous factors have a strong impact on reproductive seasonality (Gethöffer, Sodeikat & Pohlmeier 2007). A short period of high food availability leads to highly synchronous births, even in relatively harsh environmental conditions, while wild boar females that exploit low-quality food items appear to be able to give birth at any time of the year (Santos *et al.* 2006). Studies on other urban wildlife species revealed that urban environments can lead to shifts in reproduction time, scrub-jays (*Apelocoma spec.*) were for example recorded to breed three weeks earlier (Ditchkoff, Saalfeld & Gibson 2006). Therefore, differences in body weight could also be a hint for differences in juvenile age-as a result of the urban environments- and with that an indirect hint for habitat quality.

Measurements of the probability of female wild boar to reproduce (measured by presence of active follicles or pregnancy) in different groups of our study area revealed that wild boar in the city (BE) had the highest probability to reproduce, followed by females from the Grunewald forest (GW). Wild boar from Koepenick (KO) had the lowest probability to be reproducing (Fig. S 6.1.2), also fitting the habitat model (Fig. S 6.2.1).

Therefore it is possible to consider the city of Berlin as an attractive sink with high abundance of resources and a population density below carrying capacity due to high human induced mortality (Delibes, Ferreras & Gaona 2001; Naves *et al.* 2003), so that rural dispersers from the source habitats in Brandenburg can occupy the empty spaces. The urban islands, i.e. the urban forests, seem to be good habitats with a balanced ratio between mortality and reproduction.

5.4. THE TRADE-OFF BETWEEN FOOD AND FEAR IN URBAN AREAS: COSTS AND BENEFITS

Wildlife species in general are well known to avoid the human induced landscape of fear and have the ability to learn and respond to differing levels of predation risk (Laundre J. W., Hernandez L. & Ripple W. J. 2010; Johnson *et al.* 2015). The avoidance behaviour can have numerous costs, for example, elk (*Alces alces*) are more vigilant near human disturbance, resulting in decreased forage intake and reduced reproductive success (Ciuti *et al.* 2012). But since disturbance is not homogenous in space and time (Lone *et al.* 2014) wildlife are known to distinguish between different types of disturbance: Black bears were shown to avoid paved roads during the non-hunting season and moved closer to paved roads in the hunting season in order to avoid forest roads which were used by hunters (Stillfried *et al.* 2015). Roe deer (*Capreolus capreolus*) selected different habitats types to hide either from natural or human predators which differ in their “hunting strategies” (Lone *et al.* 2014). And elk (*Alces alces*) behaviour is not just influenced by the number of people but also the type of human activity, because recreational activities have a lower impact than hunters (Ciuti *et al.* 2012).

Rural wild boar in my study area have to deal with a high hunting pressure, especially in winter. Recreational activities within the rural forests, especially at public bathing spots are increasing in summer, but occur on a lower level than in the urban forests which have 1 million visits of people every year (BDF 2015; Franusch 2015). Behaviour of rural wild boar reminds to that of other wildlife species, since they avoid areas with a high human induced disturbance, especially roads and public bathing spots. In winter, when the hunting pressure was increased, wild boar often selected swamp areas close to bathing sites as resting sites (Manuscript 2). This shows an understanding of spatial and temporal shifts in the landscape of fear and a behavioural reaction by selecting areas with a decreased disturbance, such as black bears do (Stillfried *et al.* 2015). I was able to track some rural individuals during drive and single hunts. Their reactions switched from remaining within their common home ranges and a shift of the home range into a new territory (observed for female “IZW 2” after a single hunt and for female “IZW 12” after a drive hunt, Fig. S 6.1.3 A-B). The female that left her territory after the drive hunt was thereafter shot within the new area during another drive hunt, whereas the female that left her home range after a single hunt came back into the old home range after a week (Fig. S3). Wild boar from the rural forest in Brandenburg in addition reacted very sensitive to the trapping with manually activated traps. In numerous trials wild boar noticed the trapping team, escaped, did not enter the trap and avoided the trapping

location for up to two weeks even though camera trapping before the trial showed daily wild boar activity at the trap. After successful trapping and collaring, only one out of 6 rural wild boar came back to the trap, all others avoided the actual trapping location even if the trap got removed from the area (Fig. S 6.1.4).

My results show that rural wild boar have a low tolerance to the human associated landscape of fear and that the costs for avoiding disturbance are large spatial shifts and temporal adjustment of their habitat use. Since I was able to show in my Chapter 3, that the nutrition energy of stomach contents found in rural wild boar is higher than in the city of Berlin (BE) and the Koepenick forest (KO) but lower than in the Grunewald forest (GW) but body weights are higher than in both urban forests, rural wild boar might benefit from the landscape of food even though the risk of mortality is high, which leads in summary to unknown effects on animal fitness. Further studies measuring animal condition or stress could give a closer understanding in avoidance costs of the landscape of fear.

Urban forests in Berlin are different from BB and from another regarding the landscape of food and fear: While especially the western forests (Grunewald, GW and Tegel, TE) provide a high amount of deciduous mast producing forests (benefit for living in the urban forests, Manuscript 3), there are at the same time many factors which create a landscape of fear. High hunting pressure as well as a high rate of recreational activities (1 million visits annually; (BDF 2015; Franusch 2015) lead to a permanent disturbance especially during the day. In the Grunewald GW forest there are for example large dog exercising areas, where dogs are released from the lead ((Senatsverwaltung 2016), Fig. S 6.1.3,D-E). Wild boar within the Grunewald selected areas close to roads, because dog activity is decreased close to roads (personal observations). Tolerance to human activity was observed for denning wolves (*Canis lupus*) and resting lynx (*Lynx lynx*) and brown bears (*Ursus arctos*) but those species selected sites with a high cover (Sunde, Stener & Kvam 1998; Thiel, Merrill & Mech 1998; Ordiz *et al.* 2011). The fact that areas close to roads are selected as restingsites by wild boar might therefore indicate tolerance or selection of the disturbance with the least impact (roads and traffic noise vs. humans and dogs Fig. S 6.1.3 G, H). The fleeing distance in the urban forests is decreased (Chapter 2) and it is possible to regularly observe wild boar even during the day and approach them closely in the urban forests (Fig. S 6.1.3 I, F).

Wild boar in the city of Berlin were expected to benefit from attractive high energetic and easy accessible human associated food sources (Cahill *et al.* 2012; Murray *et al.* 2015;

Theimer *et al.* 2015; Tryjanowski *et al.* 2015) but in Chapter 3 I showed that urban wild boar consume natural food sources, even within the city. The landscape of fear in the city is increased due to high traffic volumes, permanent human presence and strong hunting pressure due to specialized city hunters (Manuscript 1), therefore city wild boar have high costs and need to trade-off between access to food and fear (Manuscript 2). But because urban wildlife are adapted to human-induced stresses (Ditchkoff, Saalfeld & Gibson 2006), their perception of risk might differ from that of their rural counterparts, so that the actual costs might not be as high as expected at a first look. An animal's range of movements in the urban environment reflects the costs and benefits of factors such as clumped resources, high density of conspecifics, and anthropogenic barriers of movement (Ryan & Partan 2014). The fact that home ranges of urban wild boar are smaller than those of rural individuals might therefore either reflect a good quality habitat with clumped resources or a lack of alternatives due to high competition. The fact that the landscape of food is used by urban wild boar (such as city forest wild boar), which rest (and even forage) close to roads and forage close to houses (Fig. S 6.1.3 I-N) can mean that the perception of risk is different. The behavioural flexibility ability in urban animals in general (Lowry, Lill & Wong 2013) and wild boar in specific (Keuling, Stier & Roth 2008; Keuling, Stier & Roth 2009; Ohashi *et al.* 2013) might help urban wild boar to distinguish between different human induced disturbance stimuli, such as elk responding differently to cars, recreational humans and hunters (Ciuti *et al.* 2012). Due to the permanent presence of human pedestrians and cars, wild boar in the city such as in urban forests do not show a cost-intense fleeing behaviour such as rural wild boar (measured by the decreased flight distance, Manuscript 2). Personal observations of collared city wild boar further show a tolerance towards cars, as they were regularly observed to forage next to the road (Fig. 6.1.3 A-F). In contrast to rural wild boar which avoided trapping locations after they got caught and collared, all wild boar which were collared in the urban environment regularly came back to the trapping locations (Fig. S 6.1.4). Two individuals were even caught twice and others were observed with camera traps by re-entering traps.

To trade-off between food and fear, city wild boar therefore show a high tolerance towards disturbance meaning high costs from the perspective of a rural wild boar (Fig. 5.2). In addition, the benefits of life in the city are not, as expected, high energetic human-associated food sources, but mostly natural foods. But the fact that body weights are highest in Berlin (BE) and that the probability for females to be able to reproduce and being pregnant is an indirect hint that city wild boar benefit from life in the city. It is possible to consider that the benefits are a result of decreased costs: From the perspective of a city wild boar, the perceived

landscape of fear might be low as they have learned to deal with human presence - without the need of cost-intense escape behaviours (Fig.5.2).

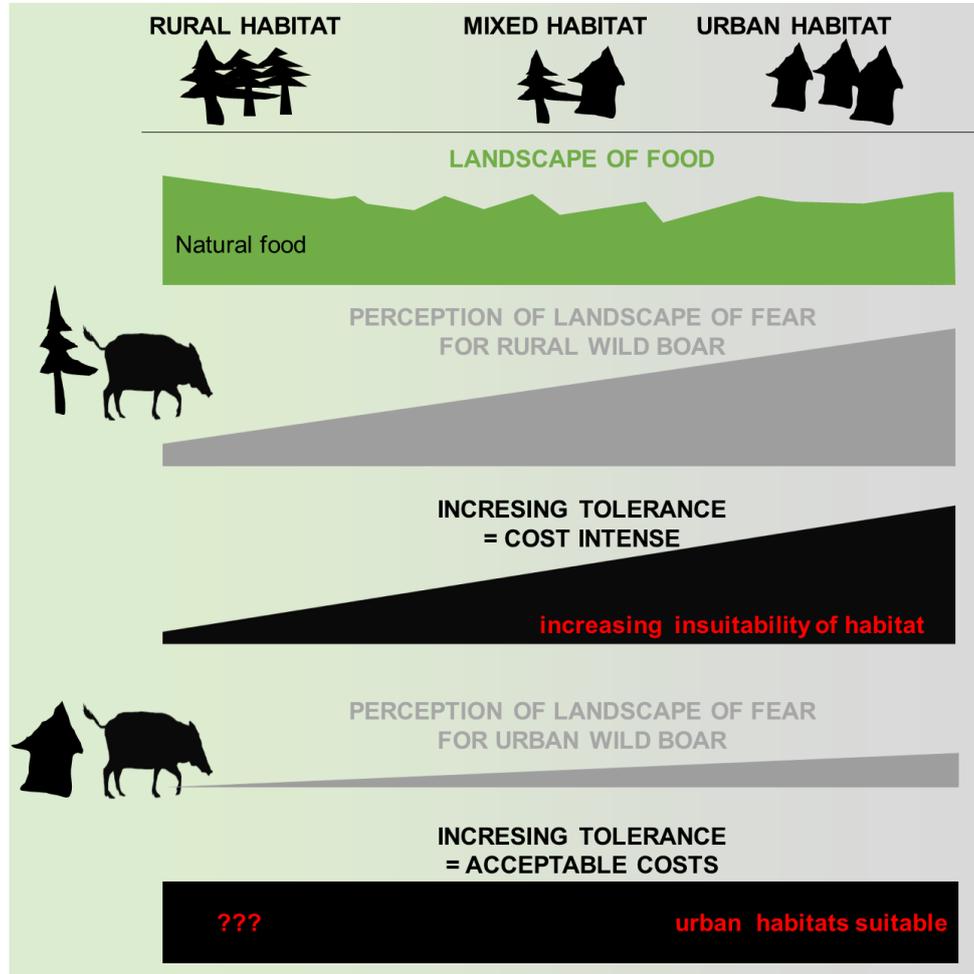


Fig. 5.2: Conceptual framework to describe an animal decision’s trade-off between the landscape of food and the landscape of fear, first from the perspective of a rural and second from the perspective of an urban wild boar.

Studies on human-induced stress in urban mammals are missing. But in tree lizards (*Urosaurus ornatus*) baseline and stress-induced corticosterone concentrations were significantly lower in urban lizards relative to the rural ones, because corticosterone concentrations may have been suppressed as a result of frequent exposure to stressors, or increased access to urban resources (French, Fokidis & Moore 2008). Martin and Reale (2008) discuss that temperament (defined as individual consistency in behaviour over time and across situations) differences are highly associated with specific endocrinal responses, because reactive (i.e. docile, and non-explorative) animals show higher cortisol release in

response to a stress than do proactive individuals (i.e. active, non-docile, and highly explorative). It remains unclear, how high the costs of adjustment for urban wild boar are. The fact that city wild boar tolerate the human induced landscape of fear on a behavioural level which is avoided by rural wild boar from the same population could be a result of differences in temperament. Further studies on hormonal stress levels and temperament could reveal, if the adjustment leads to a cost-intense high stress level, or if a specific temperament in city wild boar allows them to benefit from a highly attractive urban foraging landscape without high costs due to permanent stress.

5.5. CONCLUSION

In my thesis, I analysed in detail the ecology of wild boar in urban environments from coarse to small scale, including population genetic analyses, habitat use and foraging characteristics. My results clearly revealed that the grouping into rural, urban forest and city wild boar, which was conducted prior to the analysis, is a poor classification, because the underlying dynamics are more complex. Rural wild boar and urban wild boar which seem to be most different regarding their behaviour towards human induced disturbance (reflected by intense use of human associated landscape structures) are -genetically considered- one population with a large behavioural spectrum. Since three urban forests harbour three isolated populations whereof two of them origin directly from the rural population, shows that colonization of urban forests took place at different spatial levels. Food availability, consumed energy and body condition differ in the two urban forests which split directly from the rural group, and only the Grunewald (and Tegel) forest was bordered by the Berlin wall, which might have played a role by forming the isolated group. The trade-off between the landscape of food and fear and the resulting increase in tolerance towards human disturbance was significantly higher in urban wild boar, which were a group of city wild boar and urban forest wild boar from the Grunewald. Further studies, should consider to collar wild boar in all urban forests to be able to compare behavioural adjustment between the urban forests and between urban forests and the city. In addition, extensive measurements of body condition and stress level would help to measure real costs and benefits of different levels of urbanization. In general, my results show the complexity of the ecology of urban wildlife and how important it is to conduct analyses on different scales in order to get a broad understanding.

5.6. REFERENCES

- Amici, A., Serrani, F., Rossi, C.M. & Primi, R. (2012) Increase in crop damage caused by wild boar (*Sus scrofa* L.): the "refuge effect". *Agronomy for Sustainable Development*, **32**, 683-692.
- Baker, P.J., Bentley, A.J., Ansell, R.J. & Harris, S. (2005) Impact of predation by domestic cats *Felis catus* in an urban area. *Mammal Review*, **35**, 302-312.
- BDF, B.D.F. (2015) <https://www.berlin.de/tourismus/nachrichten/3688703-1721038-grunewald-ist-waldgebiet-des-jahres-2015>.
- Bechet, A., Giroux, J.-F. & Gauthier, G. (2004) The effects of disturbance on behaviour, habitat use and energy of spring staging snow geese. *Journal of Applied Ecology*, **41**, 689-700.
- Benhaïem, S., Delon, M., Lourtet, B., Cargnelutti, B., Aulagnier, S., Hewison, A.M., Morellet, N. & Verheyden, H. (2008) Hunting increases vigilance levels in roe deer and modifies feeding site selection. *Animal Behaviour*, **76**, 611-618.
- Beninde, J., Veith, M. & Hochkirch, A. (2015) Biodiversity in cities needs space: a meta-analysis of factors determining intra-urban biodiversity variation. *Ecology Letters*, **18**, 581-592.
- Berlin, S.f.S.u.U. (2015) Alters und Bestandsstruktur der Wälder www.stadtentwicklung.berlin.de/umwelt/umweltatlas/e_text/kb504.doc.
- Bieber, C. & Ruf, T. (2005) Population dynamics in wild boar *Sus scrofa*: ecology, elasticity of growth rate and implications for the management of pulsed resource consumers. *Journal of Applied Ecology*, **42**, 1203-1213.
- Blair, R.B. (1996) Land use and avian species diversity along an urban gradient. *Ecological Applications*, **6**, 506-519.
- Bonnot, N., Morellet, N., Verheyden, H., Cargnelutti, B., Lourtet, B., Klein, F. & Hewison, A.J.M. (2013) Habitat use under predation risk: hunting, roads and human dwellings influence the spatial behaviour of roe deer. *European Journal of Wildlife Research*, **59**, 185-193.
- Brown, J.S., Laundre, J.W. & Gurung, M. (1999) The ecology of fear: Optimal foraging, game theory, and trophic interactions. *Journal of Mammalogy*, **80**, 385-399.
- Cahill, S., Llimona, F., Cabaneros, L. & Calomardo, F. (2012) Characteristics of wild boar (*Sus scrofa*) habituation to urban areas in the Collserola Natural Park (Barcelona) and comparison with other locations. *Animal Biodiversity and Conservation*, **35**, 221-233.
- Cahill, S., Llimona, F. & Gracia, J. (2003) Spacing and nocturnal activity of wild boar *Sus scrofa* in a Mediterranean metropolitan park. *Wildlife Biology*, **9**, 3-13.
- Charnov, E.L. (1976) Optimal foraging, the marginal value theorem. *Theoretical Population Biology*, **9**, 129-136.
- Chiari, M., Ferrari, N., Bertoletti, M., Avisani, D., Cerioli, M., Zanoni, M., Alborali, L.G., Lanfranchi, P., Lelli, D., Martin, A.M. & Antonio, L. (2015) Long-Term Surveillance of Aujeszky's Disease in the Alpine Wild Boar (*Sus scrofa*). *Ecohealth*, **12**, 563-570.
- Chittka, L., Skorupski, P. & Raine, N.E. (2009) Speed-accuracy tradeoffs in animal decision making. *Trends in Ecology & Evolution*, **24**, 400-407.
- Ciuti, S., Northrup, J.M., Muhly, T.B., Simi, S., Musiani, M., Pitt, J.A. & Boyce, M.S. (2012) Effects of Humans on Behaviour of Wildlife Exceed Those of Natural Predators in a Landscape of Fear. *Plos One*, **7** (11), e50611.
- Conover, M.R. & Decker, D.J. (1991) wildlife damage to crops - perceptions of agricultural and wildlife professionals in 1957 and 1987. *Wildlife Society Bulletin*, **19**, 46-52.
- Cousse, S., Janeau, G., Spitz, F., Priede, I.G. & Swift, S.M. (1992) "Telemetry on free-ranging wild boars (*Sus scrofa* L.): temporal and spatial structure of daily movements." *Priede IG & Swift SM, Edits. Wildlife telemetry. London: Ellis Horwood* 693-697.
- Dardaillon, M. (1986) Seasonal variations in habitat selection and spatial distribution of wild boar (*Sus scrofa*) in the Camargue, Southern France. *Behavioural Processes*, **13**, 251-268.
- Dardaillon, M. & Beugnon, G. (1987) the influence of some environmental characteristics on the movements of wild boar *sus-scrofa*. *Biology of Behaviour*, **12**, 82-92.
- Davison, J., Huck, M., Delahay, R.J. & Roper, T.J. (2008) Urban badger setts: characteristics, patterns of use and management implications. *Journal of Zoology*, **275**, 190-200.
- Delibes, M., Ferreras, P. & Gaona, P. (2001) Attractive sinks, or how individual behavioural decisions determine source-sink dynamics. *Ecology Letters*, **4**, 401-403.
- Dias, P.C. (1996) Sources and sinks in population biology. *Trends in Ecology & Evolution*, **11**, 326-330.
- Dill, L.M. (1987) Animal decision making and its ecological consequences: the future of aquatic ecology and behaviour. *Canadian Journal of Zoology*, **65**, 803-811.

- Dinter, U. (1991) Das Raum-Zeitverhalten von Schwarzwild im Grunewald in den Sommermonaten unter besonderer Berücksichtigung menschlicher Störungen, Dissertation, Ludwig-Maximilian-Universität
- Ditchkoff, S.S., Saalfeld, S.T. & Gibson, C.J. (2006) Animal behavior in urban ecosystems: Modifications due to human-induced stress. *Urban Ecosystems*, **9**, 5-12.
- Dyck, M.G. & Baydack, R.K. (2004) Vigilance behaviour of polar bears (*Ursus maritimus*) in the context of wildlife-viewing activities at Churchill, Manitoba, Canada. *Biological Conservation*, **116**, 343-350.
- Emlen, J.M. (1966) The role of time and energy in food preference. *American Naturalist*, 611-617.
- Fernández, N., Kramer-Schadt, S. & Thulke, H.-H. (2006) Viability and risk assessment in species restoration: planning reintroductions for the wild boar, a potential disease reservoir, *Ecology and Society*, **11**(1).
- Ficetola, G.F., Bonardi, A., Mairota, P., Leronni, V. & Padoa-Schioppa, E. (2014) Predicting wild boar damages to croplands in a mosaic of agricultural and natural areas. *Current Zoology*, **60**, 170-179.
- Fischer, J.D., Schneider, S.C., Ahlers, A.A. & Miller, J.R. (2015) Categorizing wildlife responses to urbanization and conservation implications of terminology. *Conservation Biology*, **29**, 1246-1248.
- Franusch, M. (2015) Der Berliner Grunewald ist der Wald des Jahres 2015. (ed. A. Kögel). Der Tagesspiegel, 22.3.2015.
- 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. *Journal of Comparative Physiology B*, **178**, 997-1005.
- Frid, A. & Dill, L. (2002) Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology*, **6** (1).
- Gehrt, S.D., Anchor, C. & White, L.A. (2009) Home range and landscape use of coyotes in a metropolitan landscape: conflict or coexistence? *Journal of Mammalogy*, **90**, 1045-1057.
- Gethöffer, F., Sodeikat, G. & Pohlmeier, K. (2007) Reproductive parameters of wild boar (*Sus scrofa*) in three different parts of Germany. *European Journal of Wildlife Research*, **53**, 287-297.
- Gloor, S., Bontadina, F., Hegglin, D., Deplazes, P. & Breitenmoser, U. (2001) The rise of urban fox populations in Switzerland. *Mammalian Biology*, **66**, 155-164.
- Graham, M.D., Douglas-Hamilton, I., Adams, W.M. & Lee, P.C. (2009) The movement of African elephants in a human-dominated land-use mosaic. *Animal Conservation*, **12**, 445-455.
- Grinder, M.I. & Krausman, P.R. (2001) Home range, habitat use, and nocturnal activity of coyotes in an urban environment. *Journal of Wildlife Management*, **65**, 887-898.
- Heidiger, H. (1934) Zur Biologie und Psychologie der Flucht bei Tieren. *Biologisches Zentralblatt*.
- Hernández, L. & Landré, J.W. (2005) Foraging in the 'landscape of fear' and its implications for habitat use and diet quality of elk *Cervus elaphus* and bison *Bison bison*. *Wildlife Biology*, **11**, 215-220.
- Hespeler, B. (2007) Leitlinie Jagd im urbanen Raum von Berlin. *Senatsverwaltung fuer Stadt und Umwelt, Berliner Forsten*.
- Hobbs, N.T. & Hanley, T.A. (1990) Habitat evaluation: do use/availability data reflect carrying capacity? *The Journal of Wildlife Management*, 515-522.
- Hsu, M.J., Kao, C.C. & Agoramorthy, G. (2009) Interactions between Visitors and Formosan Macaques (*Macaca cyclopis*) at Shou-Shan Nature Park, Taiwan. *American Journal of Primatology*, **71**, 214-222.
- Hughes, J. & Macdonald, D.W. (2013) A review of the interactions between free-roaming domestic dogs and wildlife. *Biological Conservation*, **157**, 341-351.
- Janeau, G., Cousse, S., Cargnelutti, B. & Spitz, F. (1995) role of daily movements in the sociospatial organization of wild boar populations (*Sus scrofa* L.). *Revue D Ecologie-La Terre Et La Vie*, **50**, 35-48.
- Jansen, A., Luge, E., Guerra, B., Wittschen, P., Gruber, A.D., Loddenkemper, C., Schneider, T., Lierz, M., Ehlert, D., Appel, B., Stark, K. & Noeckler, K. (2007) Leptospirosis in urban wild boars, Berlin, Germany. *Emerging Infectious Diseases*, **13**, 739-742.
- Jarolimek, J., Vanek, J., Jezek, M., Masner, J. & Stoces, M. (2014) The telemetric tracking of wild boar as a tool for field crops damage limitation. *Plant Soil and Environment*, **60**, 418-425.
- Jayakody, S., Sibbald, A.M., Gordon, I.J. & Lambin, X. (2008) Red deer *Cervus elephus* vigilance behaviour differs with habitat and type of human disturbance. *Wildlife Biology*, **14**, 81-91.
- Johnson, D.H. (1980) The comparison of usage and availability measurements for evaluating resource preference. *Ecology*, **61**, 65-71.

- Johnson, H., Breck, S., Baruch-Mordo, S., Lewis, D., Lackey, C., Wilson, K., Broderick, J., Mao, J. & Beckmann, J. (2015) Shifting perceptions of risk and reward: Dynamic selection for human development by black bears in the western United States. *Biological Conservation*, **187**, 164-172.
- Johnson, M.D. (2007) Measuring habitat quality: a review. *The Condor*, **109**, 489-504.
- Keuling, O., Stier, N. & Roth, M. (2008) Annual and seasonal space use of different age classes of female wild boar *Sus scrofa* L. *European Journal of Wildlife Research*, **54**, 403-412.
- Keuling, O., Stier, N. & Roth, M. (2009) Commuting, shifting or remaining? Different spatial utilisation patterns of wild boar *Sus scrofa* L. in forest and field crops during summer. *Mammalian Biology*, **74**, 145-152.
- Keuling, O., Strauss, E. & Siebert, U. (2016) Regulating wild boar populations is "somebody else's problem"! - Human dimension in wild boar management. *Science of the Total Environment*, **554**, 311-319.
- Kopetzki, S. (2016) personal communication with the hunting consultant of Berlin about wild boar hunting strategies in Berlin.
- Kotulski, Y. & König, A. (2008) Conflicts, crises and challenges: wild boar in the Berlin City—a social empirical and statistical survey. *Natura Croatica*, **17**, 233-246.
- Krebs, J.R. (1978) Optimal foraging: decision rules for predators. *Behavioural ecology: An evolutionary approach*, 23-63.
- Laundre J. W., Hernandez L. & Ripple W. J. (2010) The Landscape of Fear: Ecological Implications of Being Afraid. *The Open Ecological Journal*, **3**, 1-7.
- Laundre, J.W., Hernandez, L., Lopez Medina, P., Campanella, A., Lopez-Portillo, J., Gonzalez-Romero, A., Grajales-Tam, K.M., Burke, A.M., Gronemeyer, P. & Browning, D.M. (2014) The landscape of fear: the missing link to understand top-down and bottom-up controls of prey abundance? *Ecology*, **95**, 1141-1152.
- Laznik, Z. & Trdan, S. (2014) Evaluation of different soil parameters and wild boar (*Sus scrofa* L.) grassland damage. *Italian Journal of Animal Science*, **13**, 7.
- Lewis, D.L., Baruch-Mordo, S., Wilson, K.R., Breck, S.W., Mao, J.S. & Broderick, J. (2015) Foraging ecology of black bears in urban environments: guidance for human-bear conflict mitigation. *Ecosphere*, **6**, 1-18.
- Lima, S.L. (1998) Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. *Advances in the Study of Behavior*, **27**, 215-290.
- Lima, S.L. & Dill, L.M. (1990) Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, **68**, 619-640.
- Lone, K., Loe, L.E., Gobakken, T., Linnell, J.D., Odden, J., Remmen, J. & Mysterud, A. (2014) Living and dying in a multi-predator landscape of fear: roe deer are squeezed by contrasting pattern of predation risk imposed by lynx and humans. *Oikos*, **123**, 641-651.
- Lowry, H., Lill, A. & Wong, B.B.M. (2013) Behavioural responses of wildlife to urban environments. *Biological Reviews*, **88**, 537-549.
- MacArthur, R.H. & Pianka, E.R. (1966) On optimal use of a patchy environment. *American Naturalist*, 603-609.
- Maibeche, Y., Moali, A., Yahi, N. & Menard, N. (2015) Is Diet Flexibility an Adaptive Life Trait for Relictual and Peri-Urban Populations of the Endangered Primate *Macaca sylvanus*? *Plos One*, **10**, 22.
- Martin, J. & Réale, D. (2008) Animal temperament and human disturbance: implications for the response of wildlife to tourism. *Behavioural Processes*, **77**, 66-72.
- Massei, G., Kindberg, J., Licoppe, A., Gacic, D., Sprem, N., Kamler, J., Baubet, E., Hohmann, U., Monaco, A., Ozolins, J., Cellina, S., Podgorski, T., Fonseca, C., Markov, N., Pokorny, B., Rosell, C. & Nahlik, A. (2015) Wild boar populations up, numbers of hunters down? A review of trends and implications for Europe. *Pest Management Science*, **71**, 492-500.
- Mauget, R. (1982) Seasonality of reproduction in the wild boar. *Proceedings-Easter School in Agricultural Science, University of Nottingham*.
- McKinney, M.L. (2002) Urbanization, biodiversity, and conservation. *Bioscience*, **52**, 883-890.
- Merkle, J.A., Robinson, H.S., Krausman, P.R. & Alaback, P. (2013) Food availability and foraging near human developments by black bears. *Journal of Mammalogy*, **94**, 378-385.
- Morelle, K., Lehaire, F. & Lejeune, P. (2014) Is wild boar heading towards movement ecology? A review of trends and gaps. *Wildlife Biology*, **20**, 196-205.
- Morelle, K., Podgorski, T., Prevot, C., Keuling, O., Lehaire, F. & Lejeune, P. (2015) Towards understanding wild boar *Sus scrofa* movement: a synthetic movement ecology approach. *Mammal Review*, **45**, 15-29.

- Murray, M., Cembrowski, A., Latham, A.D.M., Lukasik, V.M., Pruss, S. & St Clair, C.C. (2015) Greater consumption of protein-poor anthropogenic food by urban relative to rural coyotes increases diet breadth and potential for human-wildlife conflict. *Ecography*, **38**, 1235-1242.
- Nasiadka, P. & Janiszewski, P. (2015) Food preferences of wild boars (*Sus scrofa* L.) in the summer and early autumn expressed by the damage caused in agricultural crops. *Sylwan*, **159**, 307-317.
- Naughton-Treves, L., Treves, A., Chapman, C. & Wrangham, R. (1998) Temporal patterns of crop-raiding by primates: linking food availability in croplands and adjacent forest. *Journal of Applied Ecology*, **35**, 596-606.
- Naves, J., Wiegand, T., Revilla, E. & Delibes, M. (2003) Endangered species constrained by natural and human factors: The case of brown bears in northern Spain. *Conservation Biology*, **17**, 1276-1289.
- Nowak, D.J., Noble, M.H., Sisinni, S.M. & Dwyer, J.F. (2001) People and trees: assessing the US urban forest resource. *Journal of Forestry*, **99**, 37-42.
- Ohashi, H., Saito, M., Horie, R., Tsunoda, H., Noba, H., Ishii, H., Kuwabara, T., Hiroshige, Y., Koike, S. & Hoshino, Y. (2013) Differences in the activity pattern of the wild boar *Sus scrofa* related to human disturbance. *European Journal of Wildlife Research*, **59**, 167-177.
- Ordiz, A., Støen, O.-G., Delibes, M. & Swenson, J.E. (2011) Predators or prey? Spatio-temporal discrimination of human-derived risk by brown bears. *Oecologia*, **166**, 59-67.
- Otoni, I., de Oliveira, F.F.R. & Young, R.J. (2009) Estimating the diet of urban birds: The problems of anthropogenic food and food digestibility. *Applied Animal Behaviour Science*, **117**, 42-46.
- Patten, M.A. & Kelly, J.F. (2010) Habitat selection and the perceptual trap. *Ecological Applications*, **20**, 2148-2156.
- Pauleit, S., Jones, N., Garcia-Martin, G., Garcia-Valdecantos, J.L., Rivière, L.M., Vidal-Beaudet, L., Bodson, M. & Randrup, T.B. (2002) Tree establishment practice in towns and cities—Results from a European survey. *Urban Forestry & Urban Greening*, **1**, 83-96.
- Pierce, G.J. & Ollason, J.G. (1987) 8 reasons why optimal foraging theory is a complete waste of time. *Oikos*, **49**, 111-118.
- Podgorski, T., Bas, G., Jedrzejewska, B., Soennichsen, L., Sniezko, S., Jedrzejewski, W. & Okarma, H. (2013) Spatiotemporal behavioral plasticity of wild boar (*Sus scrofa*) under contrasting conditions of human pressure: primeval forest and metropolitan area. *Journal of Mammalogy*, **94**, 109-119.
- Pulliam, H.R. (1988) Sources, sinks, and population regulation. *American Naturalist*, **132**, 652-661.
- Pyke, G.H. (1984) Optimal foraging theory: a critical review. *Annual review of ecology and systematics*, **15**, 523-575.
- Pyke, G.H., Pulliam, H.R. & Charnov, E.L. (1977) Optimal foraging: a selective review of theory and tests. *Quarterly Review of Biology*, 137-154.
- Rodewald, A.D. & Shustack, D.P. (2008) Urban flight: understanding individual and population-level responses of Nearctic–Neotropical migratory birds to urbanization. *Journal of Animal Ecology*, **77**, 83-91.
- Rosner, S., Mussard-Forster, E., Lorenc, T. & Muller, J. (2014) Recreation shapes a "landscape of fear" for a threatened forest bird species in Central Europe. *Landscape Ecology*, **29**, 55-66.
- Ruiz, G., Rosenmann, M., Novoa, F.F. & Sabat, P. (2002) Hematological parameters and stress index in rufous-collared sparrows dwelling in urban environments. *The Condor*, **104**, 162-166.
- Rutz, C. (2008) The establishment of an urban bird population. *Journal of Animal Ecology*, **77**, 1008-1019.
- Ryan, A.M. & Partan, S.R. (2014) Urban wildlife behavior. *Urban Wildlife conservation*, pp. 149-173. Springer.
- Sáez-Royuela, C. & Telleriia, J. (1986) The increased population of the wild boar (*Sus scrofa* L.) in Europe. *Mammal Review*, **16**, 97-101.
- Santos, P., Fernández-Llario, P., Fonseca, C., Monzón, A., Bento, P., Soares, A.M.V.M., Mateos-Quesada, P. & Petrucci-Fonseca, F. (2006) Habitat and reproductive phenology of wild boar (*Sus scrofa*) in the western Iberian Peninsula. *European Journal of Wildlife Research*, **52**, 207-212.
- Schley, L. & Roper, T.J. (2003) Diet of wild boar *Sus scrofa* in Western Europe, with particular reference to consumption of agricultural crops. *Mammal Review*, **33**, 43-56.
- Schmidt, K. & Kuijper, D.P.J. (2015) A "death trap" in the landscape of fear. *Mammal Research*, **60**, 275-284.
- Senatsverwaltung (2016) Map on dog exercising areas in Berlin, Senatsverwaltung, <http://www.stadtentwicklung.berlin.de/forsten/hundeauslauf/>.

- Servanty, S., Gaillard, J.-M., Toigo, C., Brandt, S. & Baubet, E. (2009) Pulsed resources and climate-induced variation in the reproductive traits of wild boar under high hunting pressure. *Journal of Animal Ecology*, **78**, 1278-1290.
- Seto, K.C., Fragkias, M., Guneralp, B. & Reilly, M.K. (2011) A Meta-Analysis of Global Urban Land Expansion. *Plos One*, **6**, 9.
- Sönnichsen, L., Bokje, M., Marchal, J., Hofer, H., Jędrzejewska, B., Kramer-Schadt, S. & Ortmann, S. (2013) Behavioural responses of European roe deer to temporal variation in predation risk. *Ethology*, **119**, 233-243.
- Stillfried, M., Belant, J.L., Svoboda, N.J., Beyer, D.E. & Kramer-Schadt, S. (2015) When top predators become prey: black bears alter movement behaviour in response to hunting pressure. *Behavioural Processes*, **120**, 30-39.
- Stoen, O.G., Ordiz, A., Evans, A.L., Laske, T.G., Kindberg, J., Frobert, O., Swenson, J.E. & Arnemo, J.M. (2015) Physiological evidence for a human-induced landscape of fear in brown bears (*Ursus arctos*). *Physiology & Behavior*, **152**, 244-248.
- Sunde, P., Stener, S.O. & Kvam, T. (1998) Tolerance to humans of resting lynxes *Lynx lynx* in a hunted population. *Wildlife Biology*, **4**, 177-183.
- Theimer, T.C., Clayton, A.C., Martinez, A., Peterson, D.L. & Bergman, D.L. (2015) Visitation rate and behavior of urban mesocarnivores differs in the presence of two common anthropogenic food sources. *Urban Ecosystems*, **18**, 895-906.
- Thiel, R.P., Merrill, S. & Mech, L.D. (1998) Tolerance by denning wolves, *Canis lupus*, to human disturbance. *Canadian Field Naturalist*, **112**, 340-342.
- Thurfjell, H., Spong, G. & Ericsson, G. (2013) Effects of hunting on wild boar *Sus scrofa* behaviour. *Wildlife Biology*, **19**, 87-93.
- Tryjanowski, P., Skoraka, P., Sparks, T.H., Biadun, W., Brauze, T., Hetmanski, T., Martyka, R., Indykiewicz, P., Myczko, L., Kunysz, P., Kawa, P., Czyz, S., Czechowski, P., Polakowski, M., Zduniak, P., Jerzak, L., Janiszewski, T., Golawski, A., Dudus, L., Nowakowski, J.J., Wuczynski, A. & Wysocki, D. (2015) Urban and rural habitats differ in number and type of bird feeders and in bird species consuming supplementary food. *Environmental Science and Pollution Research*, **22**, 15097-15103.
- Van Horne, B. (1983) Density as a misleading indicator of habitat quality. *The Journal of Wildlife Management*, 893-901.
- Walther, F.R. (1969) Flight behaviour and avoidance of predators in Thomson's gazelle (*Gazella thomsoni* Guenther 1884). *Behaviour*, **34**, 184-220.
- Wandeler, P., Funk, S.M., Lurgiader, C.R., Gloor, S. & Breitenmoser, U. (2003) The city-fox phenomenon: genetic consequences of a recent colonization of urban habitat. *Molecular Ecology*, **12**, 647-656.

CHAPTER 6: Appendix

6.1. SUPPLEMENTARY MATERIAL FOR THE (DISCUSSION OF THE) THESIS

6.1.1. Body weight

METHODS

Body weights of juvenile wild boar (age estimated by hunters) were collected between October and February from drive hunts with a sample size of 126 individuals. Body weight was used as response variable in linear models to test the variation among different origins (including rural Brandenburg, Berlin city and the urban forests Grunewald and Koepenick). Significance of each level - within the predictor variable 'origin' - was determined by the Tukey post-hoc test (function `glht` in library `multcomp` (Hothorn, Bretz & Westfall 2008))

RESULTS

Body weights were highest in Berlin city with 36.1 ± 2.7 kg ($n= 8$) and differed significantly from body weights in the urban forest Grunewald with 27.5 ± 1.7 kg ($n= 21$) and from the urban forest Koepenick with mean 19.5 ± 1.5 kg ($n= 25$). Body weights in Brandenburg with 27.9 ± 1.7 kg ($n= 21$) were only significantly different from Koepenick (Fig. S 6.1.1).

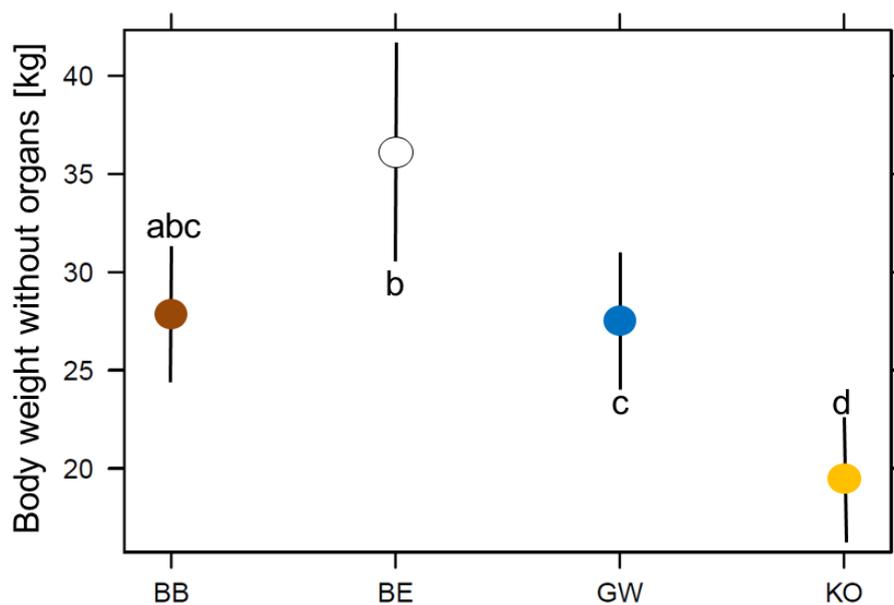


Fig. S 6.1.1: Mean body weight of wild boar juveniles in different regions of Berlin and Brandenburg. Sample size: $n=126$. Body weight was measured after removal of the organs. The regions refer to different origins, including Brandenburg (brown, BB), the urban Grunewald forest (dark blue, GW), the urban Koepenick forest (yellow, KO) and the city of Berlin (white, BE).

6.1.2. Reproduction probability of females

METHODS

The probability of female wild boar to be reproducing was investigated for 92 females which were hunted on drive hunts in Berlin and Brandenburg. An individual was classified as reproducing, if follicles within dissected ovaries were above 6mm diameter size. Probability in different regions were analysed with generalized linear models (binomial response, 0= inactive, 1= active), using different origins (including rural Brandenburg, Berlin city and the urban forests Grunewald and Koepenick) as predictor variable. Significance of each level - within the predictor variable 'origin' - was determined by the Tukey post-hoc test (function `glht` in library `multcomp` (Hothorn, Bretz & Westfall 2008))

RESULTS

The probability for females to reproduce was highest in Brandenburg with 0.62 ± 0.08 (n=32) and the urban forest Grunewald 0.60 ± 0.10 (n=20) and was not significantly different from females in Berlin 0.46 ± 0.13 (n=13). In the urban forest Koepenick, the probability to reproduce was significantly lower with 0.19 ± 0.09 (n=26) than in Brandenburg and Berlin (Fig. S 6.1.2).

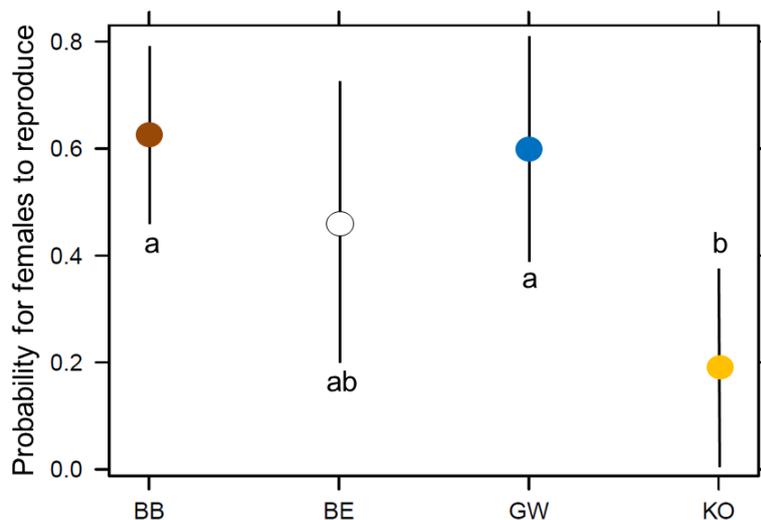
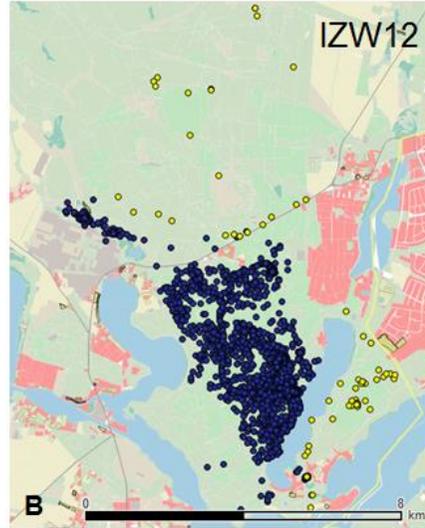
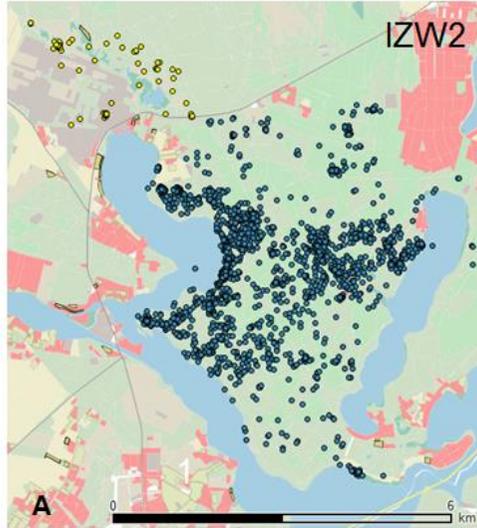


Fig. S 6.1.2: Probability of wild boar females to be reproducing in Berlin and Brandenburg. Probability in different regions were analysed with generalized linear models (binomial response, 0= inactive, 1= active). Different regions were Brandenburg (brown, BB), the urban Grunewald forest (dark blue, GW), the urban Koepenick forest (yellow, KO) and the city of Berlin (white, BE).



RURAL WILD BOAR



URBAN FOREST WILD BOAR





CITY WILD BOAR



Fig. S 6.1.3: Tolerance of disturbance in rural wild boar (A-C), urban forest wild boar (D-H) and city wild boar (I-N).

A: Locations of collared wild boar (IZW2), including excursion into a novel area after a single hunt (marked yellow), duration of stay before re-entering the previous area of activity was one week; B: locations of collared wild boar (IZW12), including escape into a novel area during a drive hunt and drifting into a new area after the drive hunt (yellow points), where she got shot on another drive hunt which took place in this areas a few days after the drive hunt in her area. Map: land cover map (detailed description in Manuscript 2); C: wild boar group in the rural forest, picture taken with a camera trap, because trials of direct observations failed.

D: typical situation at the trap within the dog exercising area of the Grunewald forest; E: Wild boar with severe leg injury after a dog attack; F: Observing a wild boar group in the Grunewald, close to our trapping location; G: View from a wild boar resting site towards the road; H: Direct observation of wild boar in the Grunewald next to a road.

I-K: Collared wild boar (IZW4) and her groups foraging next to a road; L: wild boar walking around a parking lot, M: collared wild boar (IZW4) and her group foraging in front of a house, being observed by a film team; N: Wild boar sign close to an elementary school;

Pictures A-C, H, I-K. Börner, C,D: Kameratrap, E,G;L-N: M.Stillfried.

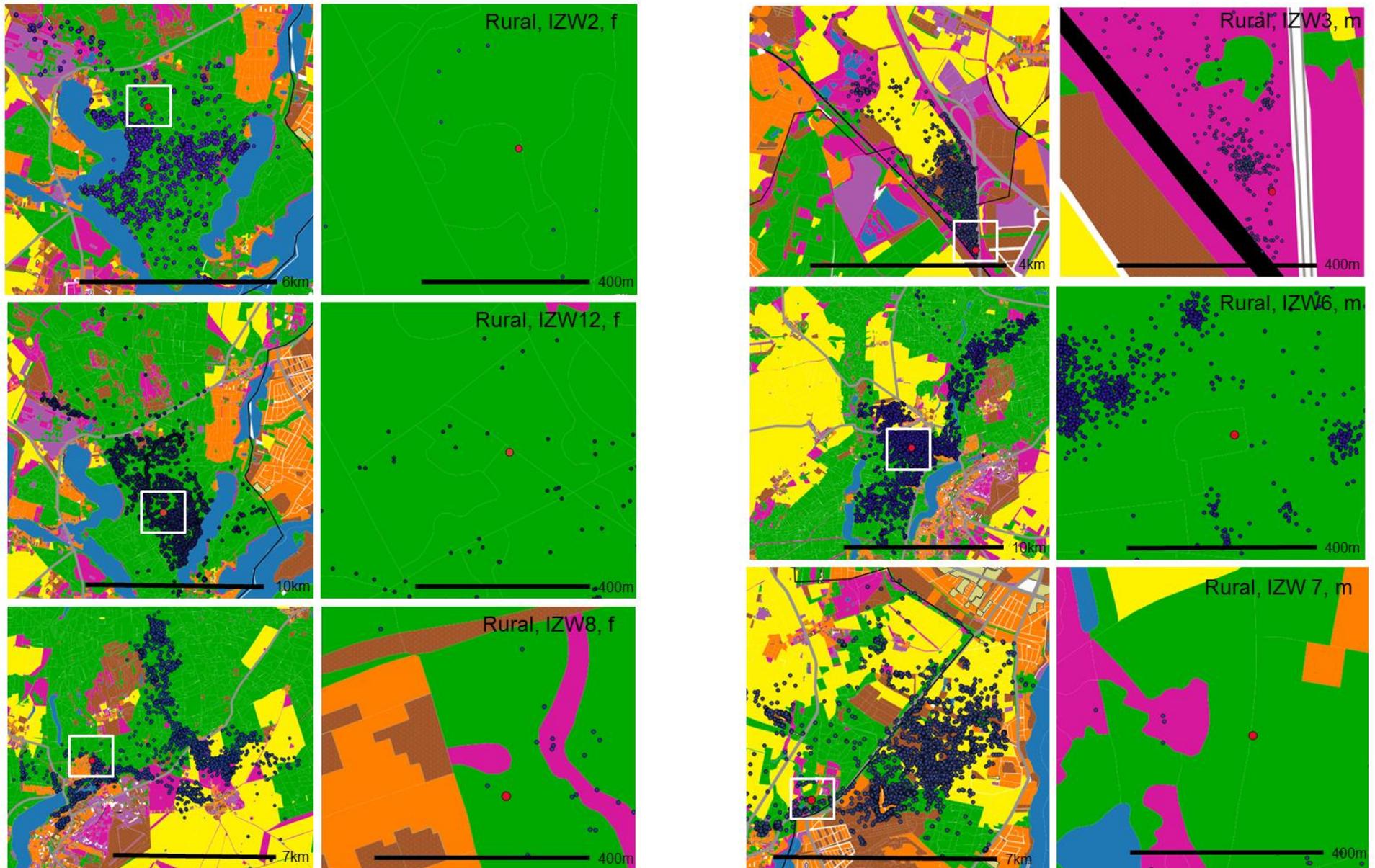




Fig. S 6.1.4: Wild boar locations (blue) and trapping locations (red) for rural and urban wild boar in Berlin and Brandenburg. The large scale picture (different scale due to different home range sizes of individuals) show the distribution of the trapping location within the area of activity. The zoomed maps (scale: 400m) show if the trapping location is visited again or if it is avoided. Map: land cover map (detailed description in Manuscript 2).

6.2. SUPPLEMENTARY INFORMATION FOR MANUSCRIPT 1

Appendix S 6.2.1: Details of the Polymerase Chain Reaction conditions

As explained in the main text, the loci were amplified in four multiplexed Polymerase Chain Reactions (PCR). All four Multiplexes were performed using the Qiagen Multiplex PCR Kit. Each reaction contained 1× QIAGEN Multiplex Master Mix and 0.1- 0.3 μm of each primer. Additionally, 1× Q-solution was added to Multiplex 4. A concentration of 100 ng DNA was used for each PCR. PCRs were started with a 5-min denaturation at 95°C, followed by 35 cycles of denaturing at 94°C for 30 s, annealing at 63°C- 55° (cycle 1: 63°, cycle 2: 61°, cycle 3: 59°, cycle 4: 57° and for the remaining 31 cycles: 55°) for 30 s and extension at 72°C for 30 s. The reaction was terminated after a final extension at 60°C for 30 min.

Tab. S 6.2.1: Properties of the microsatellite loci used in this study. System = electrophoresis loading multiplex; Chr. = chromosomal location of locus; *N* = number of samples successfully analysed; *A* = number of alleles;

Multiplex	loci	Chr.	Dye	N	Allele size range (bp)
1	S0090	12	6-Fam	387	235-255
	S0002	3	Ned	387	197-213
	S0155	1	6-Fam	387	146-158
2	S0026	16	Hex	387	93-101
	S0097	4	6-Fam	387	216-248
	Sw122	6	6-Fam	387	114-126
	Sw857	14	Hex	387	148-154
3	S0005	5	Hex	387	213-257
	S0226	2	6-Fam	387	181-191
	Sw240	2	Hex	387	94-123
	Sw632	7	Hex	387	157-177
4	Sw936	15	6-Fam	387	90-120
	SW911	9	6-Fam	387	159-167

Tab. S 6.2.2: Assignment of individual juveniles. Used loci: S0002 Sw155 Sw0090 S0097 Sw122 Sw857 S0026 Sw240 S0226 S0005 Sw632 Sw936 Sw911, Criterion: Rannala & Mountain (1997), Threshold: 0.05.

Assigned sample	Rank 1 Pop	BAPS1: GW	BAPS2: TE	BAPS3: KO	BAPS4: BB	Nb of loci
		'-log(L)	'-log(L)	'-log(L)	'-log(L)	
/boar353	BB	23.38	18.80	19.20	12.66	13
/boar350	BB	14.32	15.56	16.57	12.77	13
/boar358	BB	20.08	19.46	18.90	13.08	13
/boar359	BB	30.19	29.89	23.75	19.51	13
/boar360	BB	19.12	18.07	15.73	12.74	13
/boar361	BB	19.30	24.88	14.67	13.60	13
/boar362	BB	14.31	14.15	12.50	10.94	13
/boar363	BB	23.43	17.01	22.20	15.63	13
/boar364	BB	24.29	23.70	23.75	13.93	13
/boar115	BB	26.72	25.24	18.45	14.35	13
/boar116	KO	21.87	17.78	13.85	14.14	13
/boar121	BB	17.72	17.53	15.81	11.32	13
/boar117	BB	20.08	19.61	16.60	15.68	13
/boar118	BB	21.62	21.05	19.50	15.14	13
/boar119	KO	25.94	23.79	16.18	17.18	13
/boar355	BB	13.35	14.31	14.48	12.96	13
/boar366	BB	15.11	15.28	16.54	11.51	13
/boar725	BB	17.72	13.51	17.66	12.04	13
/boar354	BB	22.37	22.84	22.14	16.63	13
/boar356	TE	11.52	10.77	16.17	11.63	13
/boar574	GW	8.68	15.73	15.79	13.63	13
/boar348	BB	20.48	18.61	20.49	17.03	13
/boar349	BB	16.88	16.06	13.66	13.02	13
/boar370	BB	27.84	19.54	23.23	15.92	13
/boar368	BB	20.47	21.27	22.84	14.04	13
/boar369	BB	23.45	21.52	22.35	16.14	13
/boar385	GW	9.42	21.59	19.68	17.90	12*
/boar377	BB	20.75	19.81	19.63	14.09	13
/boar357	BB	15.05	19.90	19.25	14.63	13
/boar347	BB	19.85	18.00	19.29	13.47	13
/boar236	BB	16.73	19.01	16.52	11.92	13
/boar237	BB	22.25	21.22	15.68	13.80	13
/boar232	BB	16.89	15.06	14.71	12.15	13
/boar266	TE	14.14	10.89	13.23	10.97	13
/boar413	BB	18.75	19.88	17.42	13.93	13
/boar256	BB	19.32	20.10	16.17	13.48	13
/boar293	BB	13.94	14.93	14.65	11.38	13

Fig. S 6.2.1: Wild Boar Model: To assess the habitat quality for wild boar in Berlin and surrounding BB, a spatial suitability assessment was made employing a Geographic Information System (GIS)-rendered algorithm developed by Fernández, Kramer-Schadt & Thulke (2006). This algorithm is based on a regression of wild boar densities on availability of deciduous forest (Jedrzejewska et al., 1994) and gives the maximum number of breeding adult females per grid cell interpreted as the breeding capacity per core area. The original model covering regional to landscape scale applications focused on detecting possible breeding habitats for family groups of wild boar requiring an area of 4 km² (cell size) equal to the core area (Fernández et al., 2006 - and reviews therein); however, our telemetry data from collared wild boar in Berlin (unpublished data) yielded much smaller home ranges and higher densities. We therefore recalculated the density on a 1 km² scale and used the upper boundary of the regression estimates to yield breeding capacity per cell. Cells with less than 10% (minimum requirement variable) of their areas covered by forests and natural vegetation were assigned to the category of non-breeding habitat. The land cover maps that were reclassified in the following way: Forest areas, coniferous as well as deciduous, were classified as suitable breeding habitats. Natural and semi-natural vegetation, including heath land, meadows, bogs, reeds, fens and pastures, was classified as semi-suitable habitat. Finally, agricultural land in rotation was categorized as unsuitable for breeding (i.e. matrix), while lakes and urban areas were categorized as barriers to movement. The algorithm then yields a continuum of breeding capacities per grid cell based on the percentage of suitable and semi-suitable habitats. A cut-off of 25% was used for the amount of forest per cell. We obtained basic land use maps from Corine.

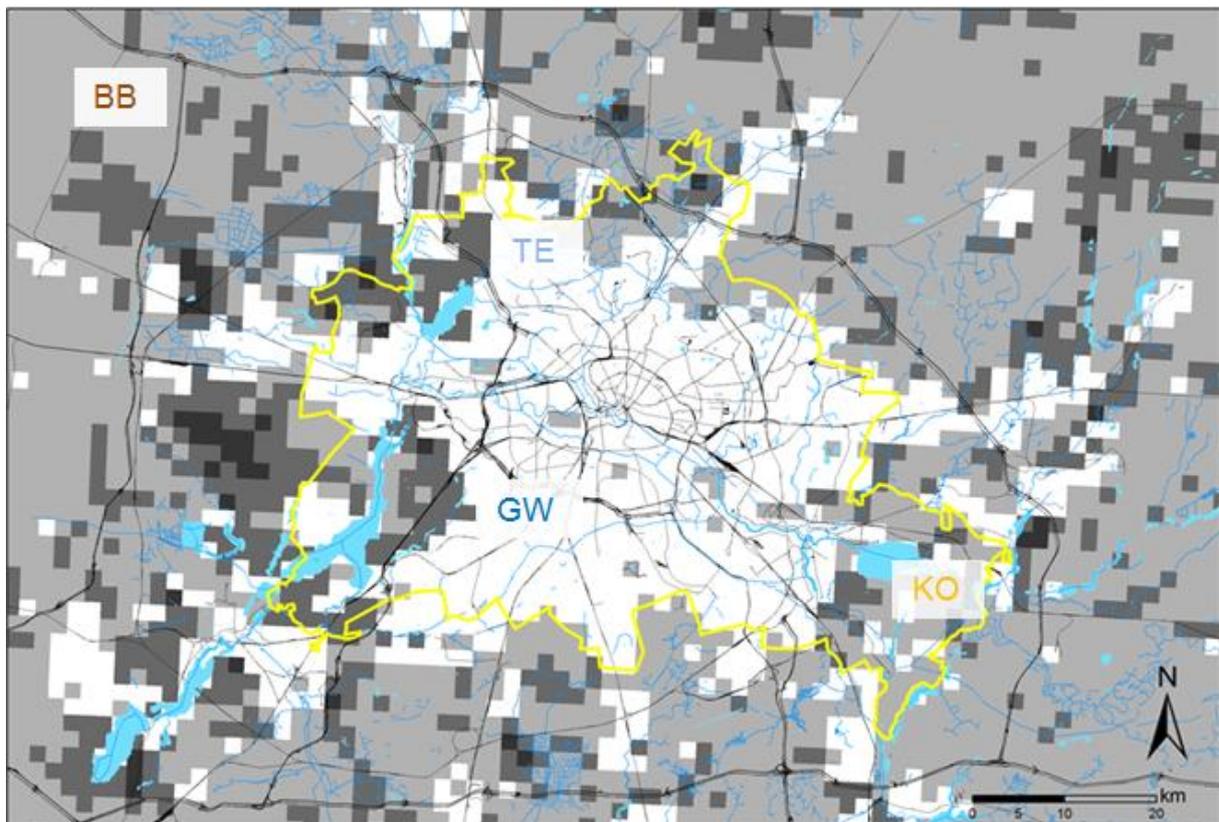


Fig. S 6.2.2: log-likelihood for STRUCTURE clusters

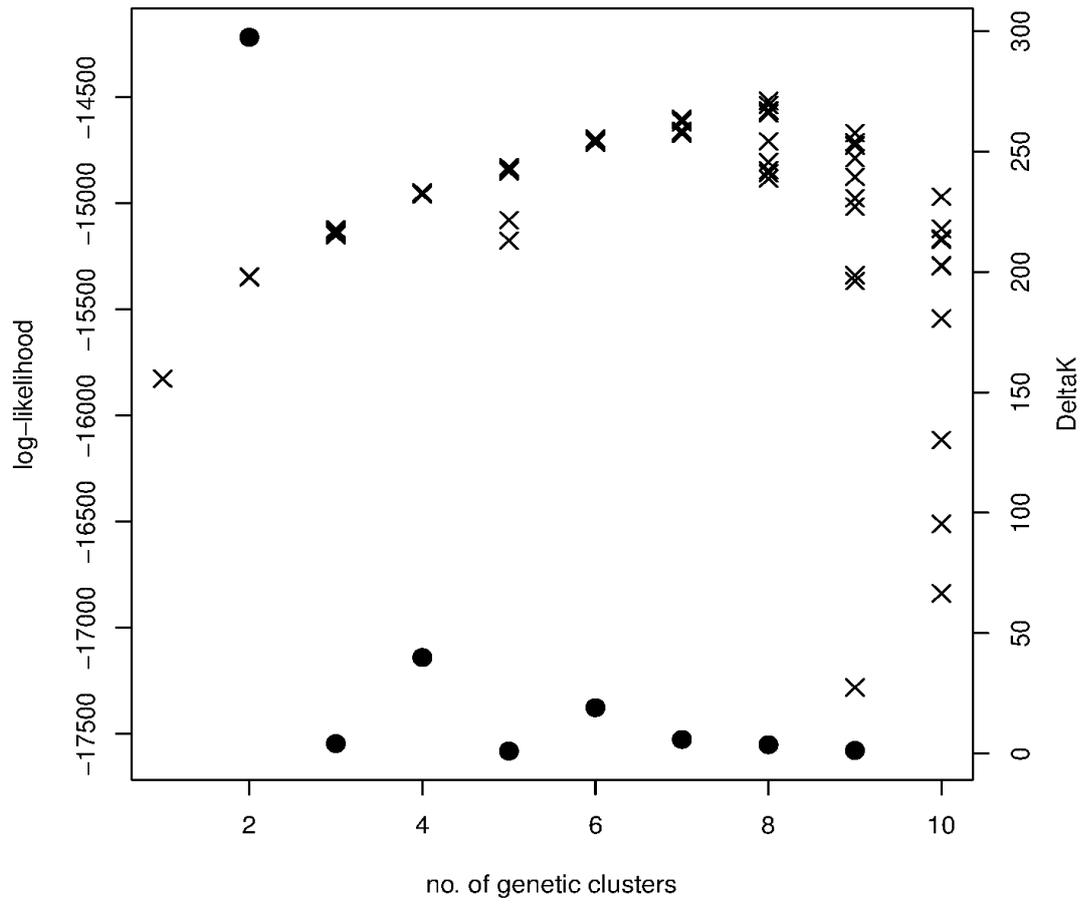


Fig. S 6.2.3: Map showing STRUCTURE results for wild boar sampled in Berlin and Brandenburg with $k=5$. Size of pie chart represents number of samples; each piece represents percentage of each cluster throughout individuals. A: Zoom into the urban Grunewald (GW) clusters (C: urban cluster Tegel (TE), D: urban cluster Koepenick (KO)). Map: OpenStreet maps.

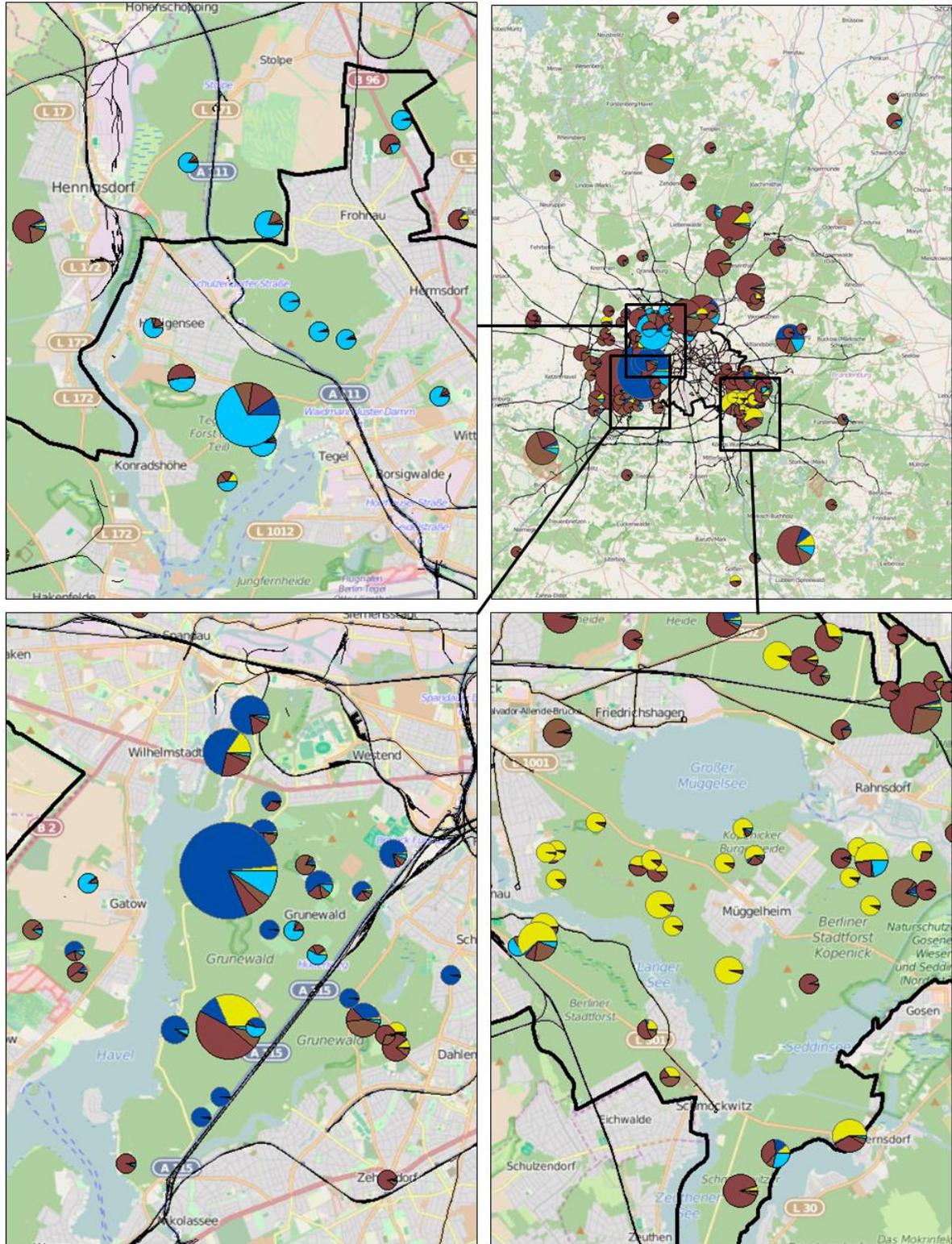


Fig. S 6.2.4: Factorial correspondence analysis of wild boars in Berlin and Brandenburg. The four pre-defined populations correspond to the clusters inferred using the spatial BAPS algorithm. Percentage of the total variation explained by each of the two axes is given.

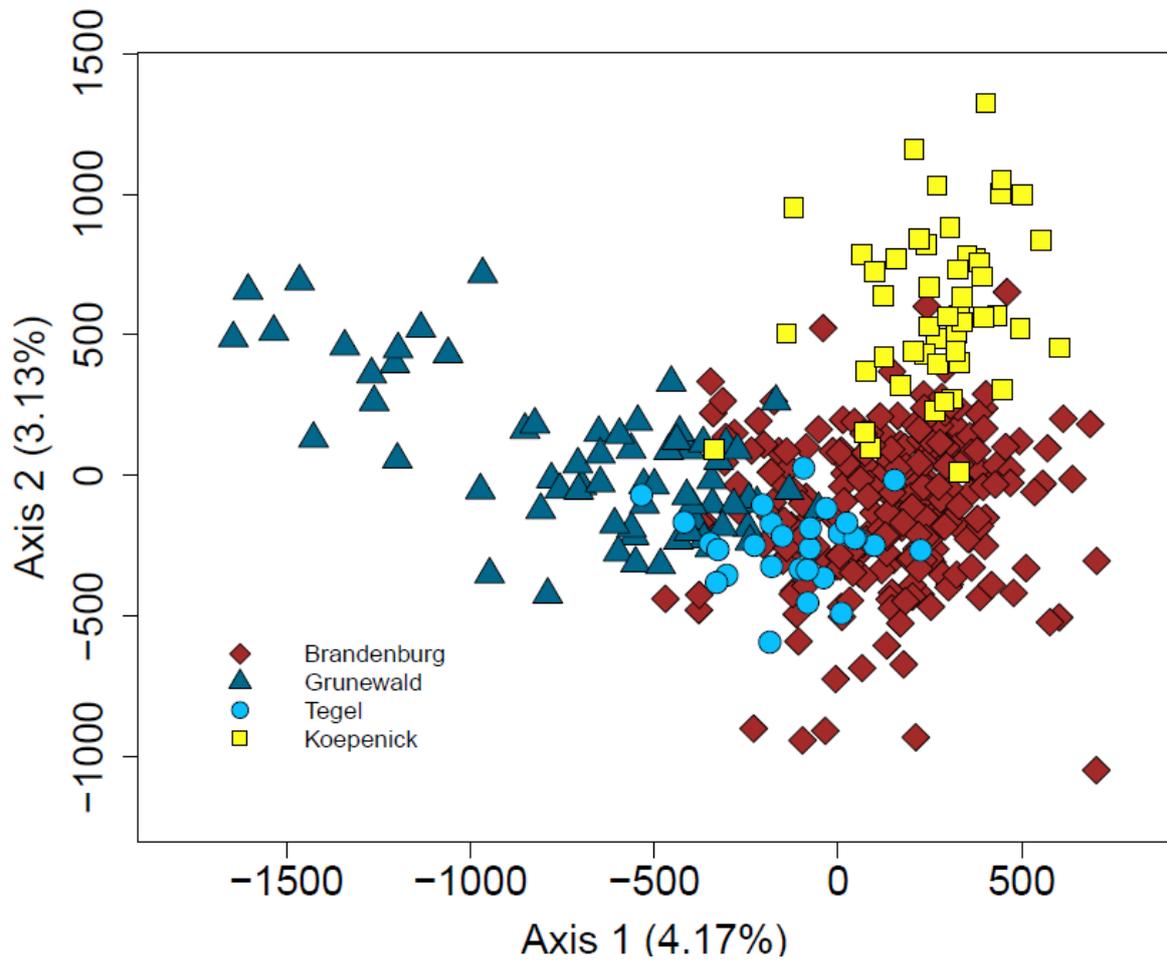
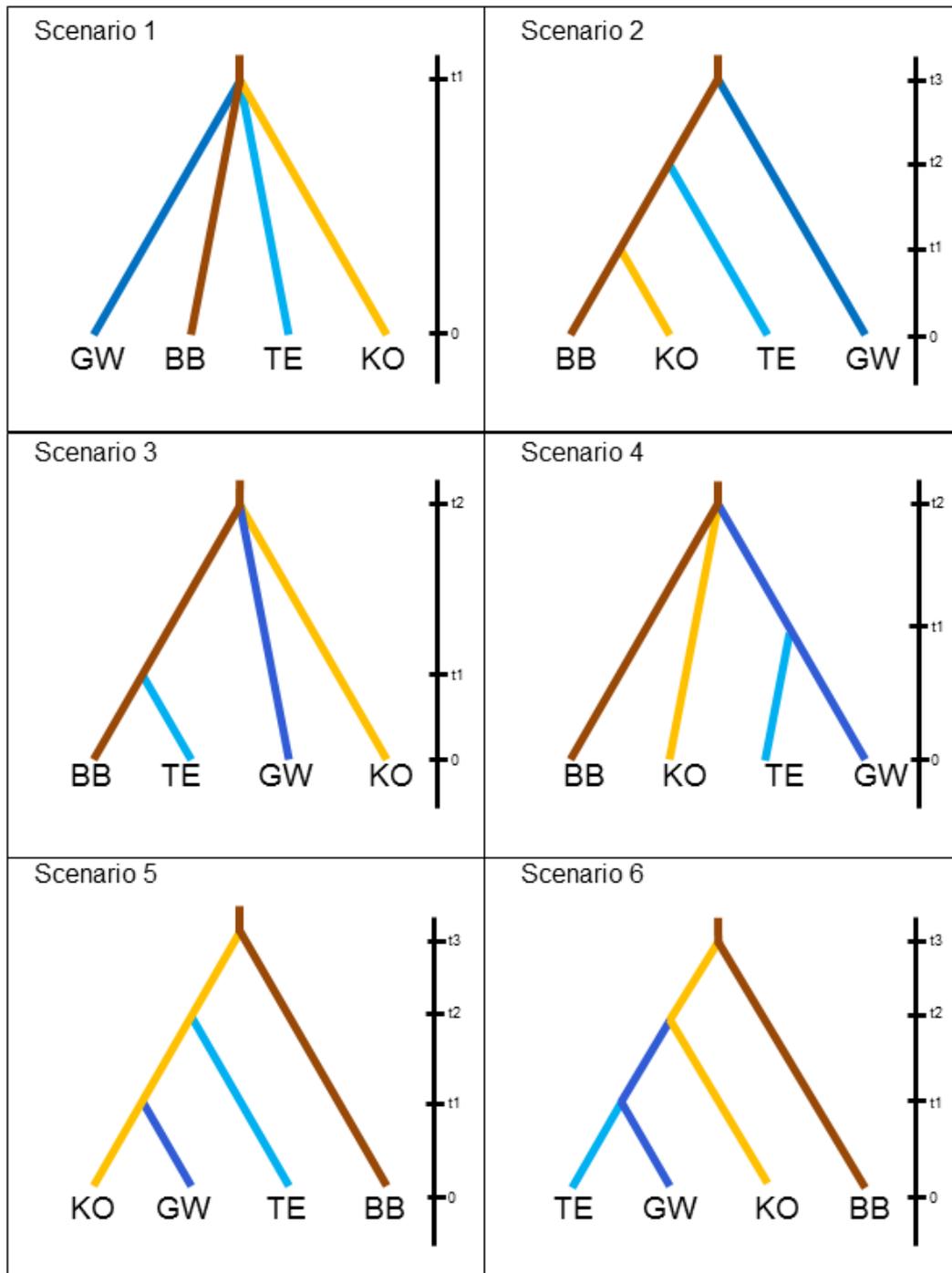
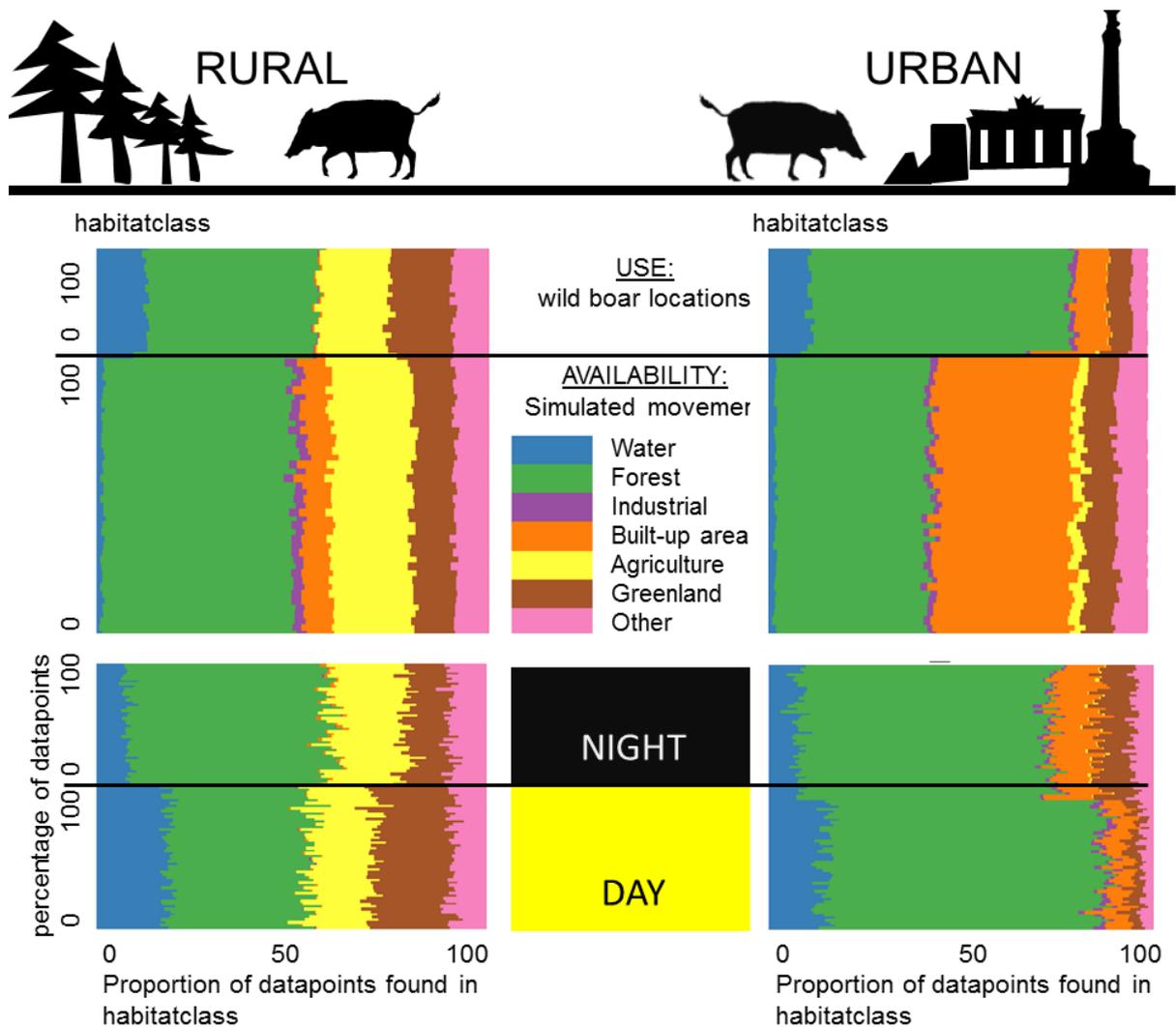


Fig. S 6.2.5: Tested DIYABC Scenarios: Scenario 1 predicts that all three urban clusters evolved independently at the same time out of the common ancestral population in Brandenburg. Scenario 2 predicts that regarding the Fst values, where Ko is closest to BB and GW far away from BB, that GW split first, TE next and KO as last group. Since the FCA analysis shows an overlap of TE and BB, scenario 3 predicts that KO and GW split at the same time and TE split later from the BB group. Scenario 4 assumes that GW and KO both split independently from BB and TE split later from the GW group due to geographical closeness and isolation during the time of the Berlin wall and because of low differentiation reflected by Fst values. Scenario 5 and scenario 6 both predict that KO first evolved out of BB. In scenario 5, TE split first from KO and GW last, in scenario 6, GW split from KO and TE last from GW. The y-axis (t) shows the time, t2 is the point when Grunewald and Koepenick split from the rural Brandenburg cluster, t1 is the time point when the Tegel cluster split from the Grunewald cluster and 0 stands for the current time.



6.3. SUPPLEMENTARY INFORMATION FOR MANUSCRIPT 2

Fig. S 6.3.1: Habitat use and movement characteristics of urban and rural wild boar in Berlin and Brandenburg, Germany, between 2013 and 2015. The main habitat categories water bodies, forest, industrial areas, housing (“built-up area”), agriculture and open green spaces are displayed in different colours. The plot shows the percentage of each habitat class on the x-axis and the percentage of locations on the y-axis to summarize the distribution of locations within different habitat classes. The use vs. availability approach displays GPS locations of wild boar (= use) in comparison with locations of simulated movement (= availability) created by simulated correlated random walks. The simulated movements represents random habitat use (wild boar = simulated locations) in contrast to habitat selection in the sense of habitat use preferences (wild boar different from simulated track). For each individual, five correlated random walks were created. To aid clarity and visual interpretation, only half of the data are displayed here – the remaining data points are similar to the displayed ones. Locations for urban and rural wild boar are displayed separately. The second part of the Fig. displays differences in habitat use by wild boar during day (= inactive times for WB, starting at 7am) and night (=active times for WB, starting at 7pm) were used.



Tab. S 6.3.1: List of candidate models for the linear mixed models (LMMs) and generalised linear mixed models GLMMs). For the second order analysis of habitat selection at the scale of total home ranges we used home range size per month [1], shift of the centroid of home ranges [2] and shift of resting sites [3] as response variables. Predictor landscape variables were percentage of forest (%Fo = food), percentage of water (%Wa = food), percentage of houses (%Ho = fear) and number of road crossing events (cross=fear) within the home range in interaction with season (SEASON = summer & winter) and origin (ORIGIN = urban & rural). Wild boar identity and month were used as random effects. The candidate models were defined to test different hypotheses. The “full” models hypothesized that home range size and shift of home range centroids and resting sites is influenced by both food and fear related landscape variables within summer and winter in urban or rural wild boar. “Food1-3” models hypothesized that only food variables in summer and winter and in urban or rural wild boar have an impact, “fear1-3” models hypothesized that only fear variables in summer and winter and in urban or rural wild boar have an impact. The “neutral” model hypothesized that only season and origin influence the response and the “intercept” model assumes that the differences are only based on random factors. [4] The next set of models compared actual wild boar locations (coded as 1) against a null model of correlated random walks (CRW, coded as 0) as binary response variable. Explanatory variables were distances to roads (D_Ro), water bodies (D_Wa), housing (D_Ho) and forest (D-Fo), season (SEASON, summer & winter), sex, daytime (DT, day & night), normalized differenced vegetation index (NDVI) and origin. [5] As binomial response, day (= inactive times for WB, starting at 7am, coded as 0) and night (=active times for WB, starting at 7pm, coded as 1) were used. Explanatory variables were the same habitat distance variables as described for the GLMMs used to model response variable [4].

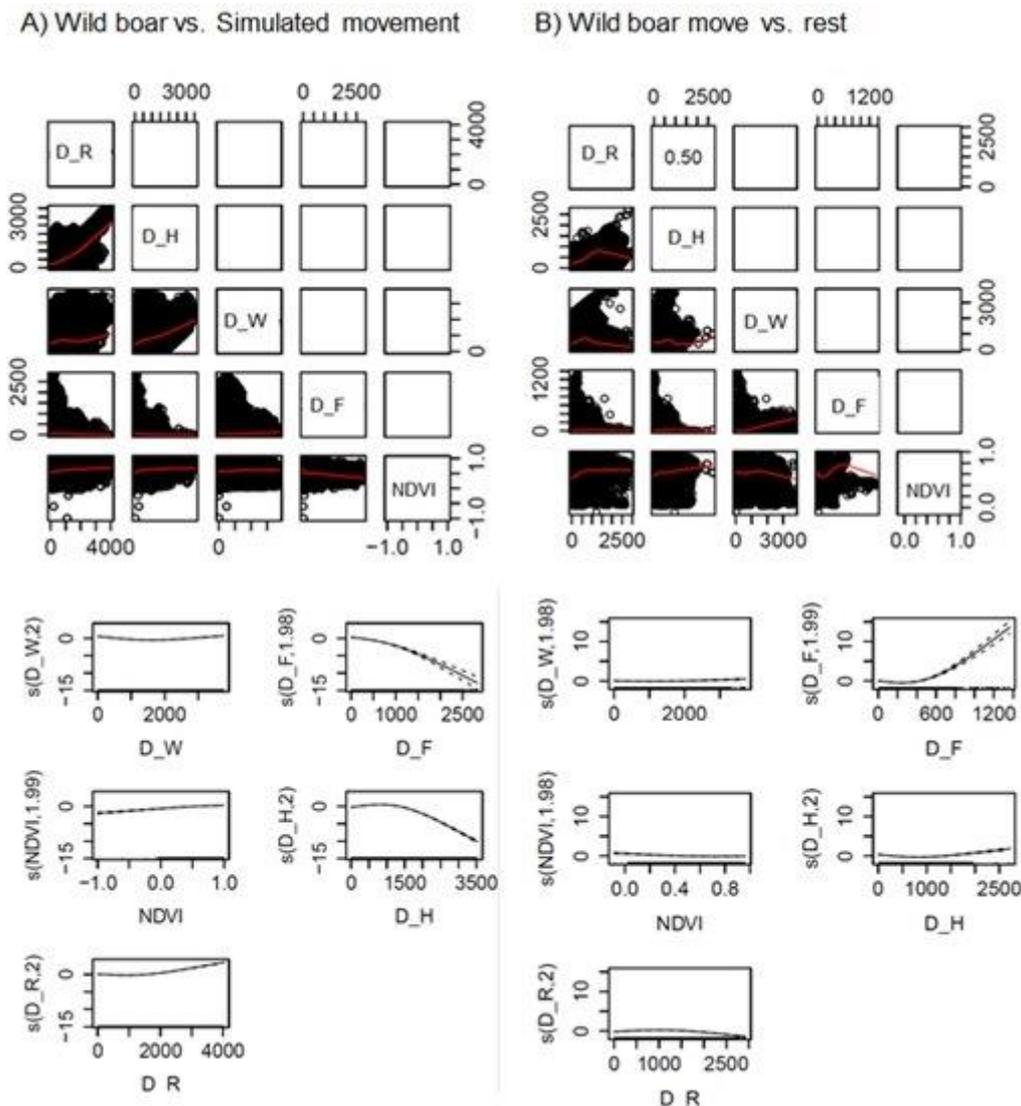
The different model types represent different hypotheses as described for [1-3] with the difference that for the model sets [4] and [5] only one “food” model and only one “fear” model were tested.

Model	Variable	Random
<i>second order habitat selection analysis</i>		
[1] LMM, Response= size of home range , n=54		
[2] LMM, Response= distance of monthly shift of home range centroids, n=54		
[3] LMM, Response= distance of shift of average monthly resting sites, n=54		
Full	%_Fo + %_Wa	+ %_Ho +cross * Season* Origin + ID + Month
Food1	%_Fo + %_Wa	* Season* Origin + ID + Month
Food2	%_Fo	* Season* Origin + ID + Month
Food3	%_Wa	* Season* Origin + ID + Month
Fear1		%_Ho + cross * Season* Origin + ID + Month
Fear2		%_Ho * Season* Origin + ID + Month
Fear3		cross * Season* Origin + ID + Month
Neutral		* Season* Origin + ID + Month
Intercept		+ ID + Month
<i>third order habitat selection analysis</i>		
[4] GLMM (binomial), Response= Wild boar actual location (1) vs. CRW (0), n=469,758		
[5] GLMM (binomial), Response= Move (1) vs. Resting (0), n= 78,293		
Full	D_Fo +D_Wa*NDVI	+D_Ho +D_Ro * Season* Origin + ID + Month
Food	D_Fo +D_Wa+NDVI	* Season* Origin + ID + Month
Fear		+D_Ho +D_Ro * Season* Origin + ID + Month
Neutral		* Season* Origin + ID + Month
Intercept		+ ID + Month

Fig. S 6.3.2: Correlation plots and generalised additive models (GAMs) to check the assumption of linearity in generalised linear mixed models. The correlation plot contains and displays the correlation coefficients between each pair of variables and is used to check whether variables are correlated. If a correlation coefficient is larger than 0.7, the two variables are considered to be highly correlated and will not be used in the same model.

GAM plots show the component smooth functions on the scale of each linear predictor. If the plot of the predictor includes a shift in direction of the slope, the variable should be used in its quadratic form, with two shifts in direction.

A) Actual wild boar movements (1) vs. simulated correlated random walk (0) as binary response variable, B) Wild boar activity, in terms of moving (1) versus resting (0) as binary response. The variables distance to water bodies (D_W), distance to housing (D_H), distance to major roads and motorways (D_R), distance to forest (D_F) and normalized differenced vegetation index (NDVI) were used in generalised mixed models (GLMMs, see Tab. S2 for detailed list of candidate models).



Tab. S 6.3.2: Full model selection Tab. for second order habitat selection analysis. Linear mixed models (LMMs) using home range size [1], shift of monthly home range centroids [2] and shifts of average monthly resting sites [3] as response variables were run. Different combinations of foraging and fear landscape variables in interaction with season (summer, winter) and origin (urban, rural) were tested. The landscape variables were percentage of forest (%F =food), percentage of water bodies (%W =food), percentage of housing (%H =fear) and number of road crossing events (cross=fear) within the home range. An explanation of the variables and their expected impact on wild boar is shown in Tab. 3.1. All candidate models including detailed explanations are listed in Tab. S.6.3.1. Df shows the degrees of freedom, AIC is the Akaike Information criterion, used for model selection, the delta shows the difference between the best fitted model and other candidate models, the w is the model weight.

CHAPTER 6: Appendix

Modelname	Intercept	%Fo	%Wa	%Ho	cross	Origin	Season	Fo * Orig	Fo * Seas	Wa * Orig	Wa * Seas	Ho * Orig	Ho * Seas	Cross * Orig	Cross * Seas	Ori * Seas	Fo*Orig*Seas	Wa*Orig*Seas	Ho*Orig*Seas	Cross*Orig*Seas	df	logLik	AICc	delta	w
[1] LMM, Response= monthly home range size, n=54																									
fear2	1.67			3.03		+	+					+	+			+		+			1	-41.06	110.71	0.00	1.00
Neutr	-0.17					+	+									+					7	-59.33	135.20	24.49	0.00
Inter	-0.03																				4	-64.35	137.55	26.83	0.00
food2	-0.35	-0.80				+	+	+	+							+	+				1	-56.12	140.83	30.12	0.00
food3	-0.09		0.85			+	+			+	+					+		+			1	-57.18	142.96	32.24	0.00
food1	-0.09	-1.06	1.22			+	+	+	+	+	+					+	+				5	-51.62	146.57	35.85	0.00
fear1	1.33			2.66	0.01	+	+					+	+	+	+	+			+	+	5	-55.68	154.70	43.99	0.00
fear3	-0.10				0.01	+	+							+	+	+				+	1	-71.70	171.99	61.28	0.00
full	2.02	-0.96	0.60	3.54	0.01	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	3	-50.64	186.71	76.00	0.00
[2] LMM, Response= shift of monthly home range centroid, n=54																									
Inter	-0.03																				4	-66.81	142.46	0.00	0.86
Neutr	0.31					+	+									+					7	-64.91	146.37	3.90	0.12
fear2	-1.35			-3.27		+	+					+	+			+			+		1	-61.12	150.83	8.37	0.01
food3	0.26		-0.28			+	+			+	+					+		+			1	-64.44	157.47	15.01	0.00
food2	0.30	-0.56				+	+	+	+							+	+				1	-64.56	157.72	15.26	0.00
food1	0.56	-1.05	0.79			+	+	+	+	+	+					+	+				5	-63.04	169.41	26.95	0.00
fear3	0.06				0.01	+	+							+	+	+				+	1	-78.54	185.68	43.21	0.00
fear1	-2.16			-4.38	0.01	+	+					+	+	+	+	+			+	+	5	-74.17	191.68	49.21	0.00
full	-1.42	-0.94	1.29	-3.34	0.01	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	3	-67.96	221.36	78.89	0.00
[3] LMM, Response= shift of average monthly resting site (RS), n=54																									
Neutr	0.29					+	+									+					7	-65.11	146.76	0.00	0.58
Inter	-0.01																				4	-69.41	147.67	0.91	0.37
fear2	0.86			1.16		+	+					+	+			+			+		1	-61.81	152.23	5.46	0.04
food2	0.26	-0.76				+	+	+	+							+	+				1	-64.16	156.92	10.15	0.00
food3	0.12		-0.33			+	+			+	+					+		+			1	-64.53	157.66	10.90	0.00
food1	0.57	-1.44	1.24			+	+	+	+	+	+					+	+				5	-61.99	167.31	20.55	0.00
fear3	-0.33				0.04	+	+							+	+	+				+	1	-76.46	181.53	34.76	0.00
fear1	-0.54			-0.45	0.04	+	+					+	+	+	+	+			+	+	5	-70.99	185.31	38.54	0.00
full	0.46	-1.43	1.93	0.82	0.05	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	3	-63.64	212.72	65.95	0.00

Tab. S 6.3.3: Full model selection Tab. for third order habitat selection analysis. Best supported generalised linear mixed models (binomial GLMM) using wild boar locations (coded as 1) vs. correlated random walks (CRW [5], coded as 0) or wild boar moving (coded as 1) vs resting (coded as 0) locations [6] as response variables. Explanatory variables were distances to roads (D_R), water bodies (D_W), housing (D_H), and forest (D_F), season (SEASON, summer & winter), normalized differenced vegetation index (NDVI) and origin (ORIGIN, rural & urban). A list of all tested models is shown in Tab. S 6.3.1.

Modelname	Intercept	D_Fo	NDVI	D_Wa	D_H0	D_R0	Origin	Season	D_Fo * Origin	D_F * Season	NDVI * Origin	NDVI * Season	D_Wa * Origin	D_Wa * Season	D_Ho * Origin	D_H0 * Season	D_R0 * Origin	D_Ro * Season	Origin * Season	D_Fo * Origin * Season	NDVI * Origin * Season	D_Wa * Origin * Season	D_Ho * Origin * Season	D_Ro * Origin * Season	Df	Loglik	Aicc	Delta	W	
[4] GLMM (binomial), Response= Wild boar vs. CRW, n=469758																														
full	-2.29	0.40	1.24	0.03	-0.23	0.23	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	26	-187821.8	375695.6	0.0	1
food	-2.27	0.43	1.25	0.00			+	+	+	+	+	+	+	+					+	+	+				18	-191655.4	383346.9	7651.2	0	
fear	-1.61				-0.23	0.24	+	+							+	+	+	+	+				+	+	14	-208374.9	416777.9	41082.2	0	
Inter	-1.61																								3	-211654.7	423315.4	47619.7	0	
Neutr	-1.61						+	+											+						6	-211654.7	423321.4	47625.7	0	
[5] GLMM (binomial), Response= Move vs. Resting, n= 78293																														
full	0.06	-0.19	0.14	-0.30	-0.07	-0.32	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	25	-52417.0	104884.0	0.0	1	
fear	0.04	-0.19	-0.09	-0.26			+	+	+	+	+	+	+	+					+	+	+			+	13	-52742.2	105518.5	634.5	0	
food	-0.03				-0.21	-0.20	+	+							+	+	+	+	+	+	+				17	-52939.8	105905.6	1021.6	0	
Neutr	-0.17						+	+											+						5	-53371.3	106752.7	1868.7	0	
Inter	-0.09																								2	-53401.7	106807.4	1923.4	0	

Fig. S 6.3.3: Probability of wild boar presence as a function of distances to habitat structures. A) comparing wild boar locations with simulated movements. The larger the probability values, the more likely it was to find wild boar close to the appropriate habitat category. B) Wild boar move vs. resting locations. The larger the probability values, the more likely it was to find wild boar close to the appropriate habitat category while they were moving. Standard deviation of the random effect “wild boar ID” = 0.201.

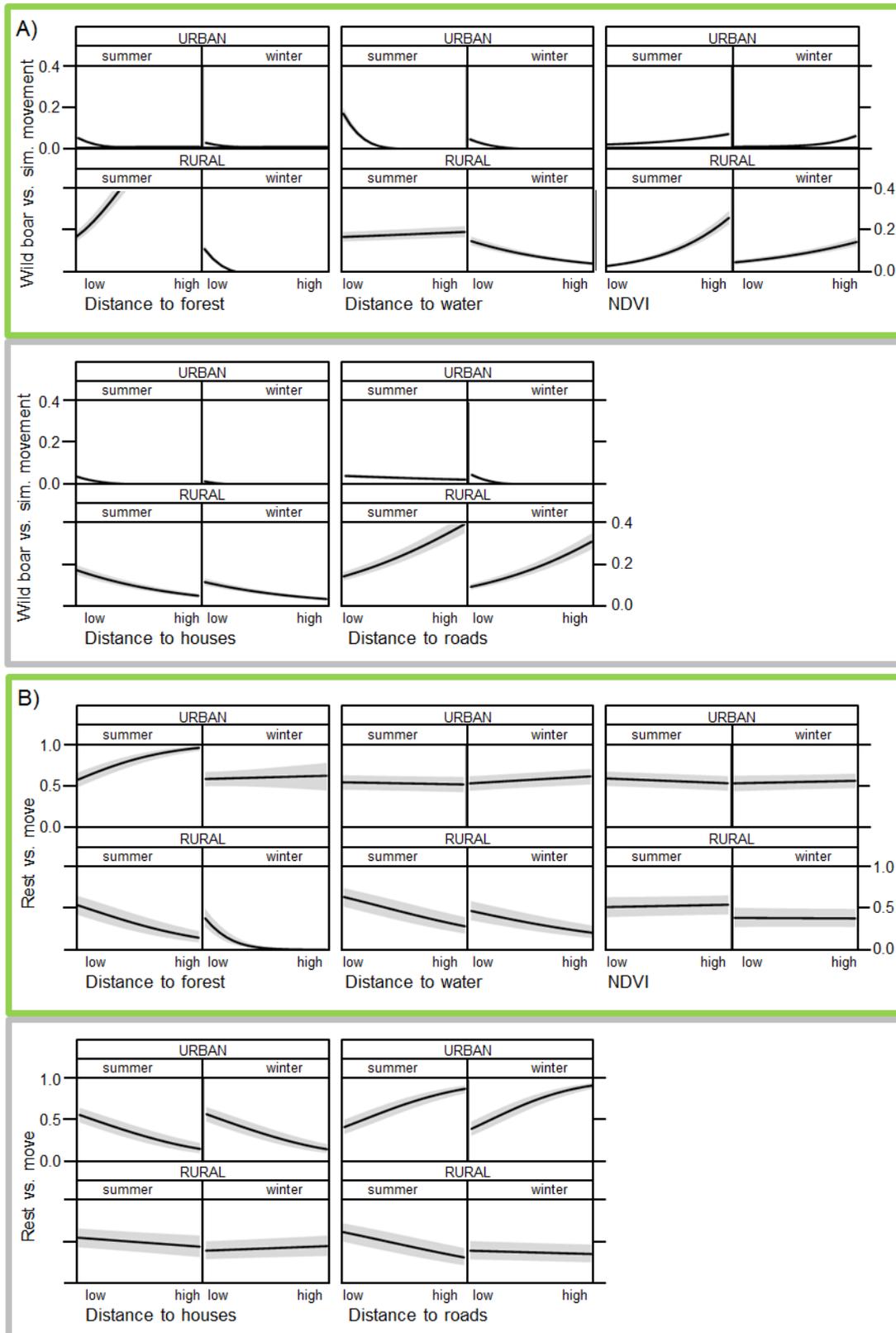
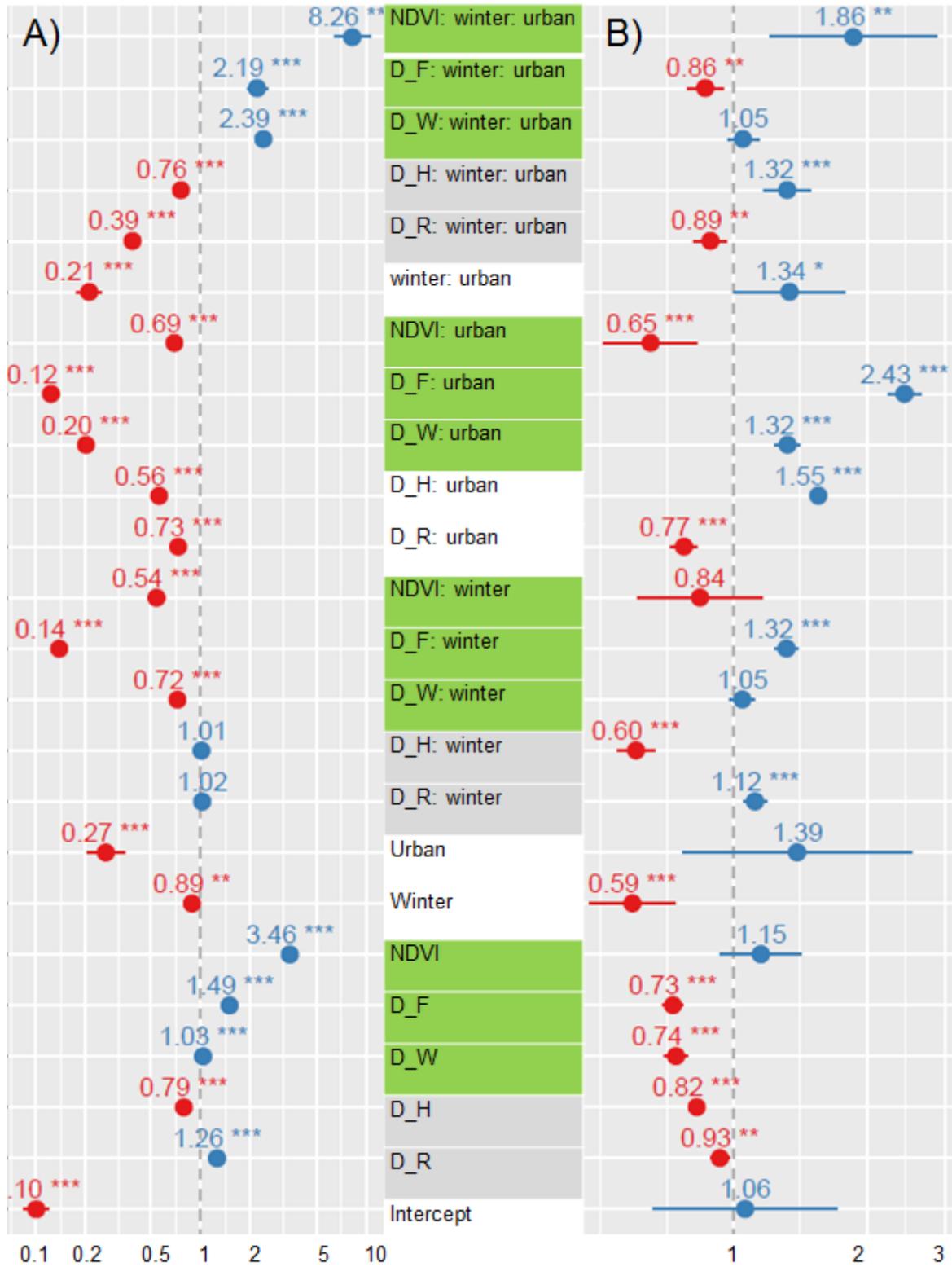


Fig. S 6.3.4: Probability of wild boar presence for the respective land use categories as predicted by the best generalised mixed model. A) testing probability of wild boar to occur close to respective habitat categories in comparison to simulated movement tracks, B) testing probability of wild boar to occur close to respective habitat categories while they move. Standard deviation of the random effect “wild boar ID” = 0.201



Tab. S 6.3.4 Estimates of model coefficients for the best models

Fixed effect	Estimate	Std. Error
<i>[4] GLMM (binomial), Response= Wild boar vs. CRW, n=469758</i>		
Intercept	-2.290	0.085
D_Road	0.228	0.009
D_Houses	-0.234	0.010
D_W	0.032	0.007
D_F	0.401	0.012
NDVI	1.240	0.037
winter	-0.121	0.041
urban	-1.322	0.129
D_R: winter	0.020	0.011
D_H: winter	0.010	0.013
D_W: winter	-0.324	0.010
D_F: winter	-1.970	0.032
NDVI: winter	-0.615	0.062
D_R: urban	-0.313	0.015
D_H: urban	-0.579	0.021
D_W: urban	-1.598	0.025
D_F: urban	-2.086	0.027
NDVI: urban	-0.367	0.056
winter: urban	-1.553	0.089
D_R: winter: urban	-0.951	0.032
D_H: winter: urban	-0.276	0.036
D_W: winter: urban	0.872	0.044
D_F: winterurban	0.783	0.071
NDVI: winter: urban	2.111	0.128
<i>B) [5] GLMM (binomial), Response= Move vs. Resting, n= 78293</i>		
Intercept	0.059	0.244
D_H	-0.072	0.024
D_F	-0.192	0.013
D_W	-0.301	0.029
D_R	-0.316	0.027
NDVI	0.141	0.108
winter	-0.528	0.112
urban	0.329	0.305
D_H: winter	0.110	0.029
D_F: winter	-0.509	0.049
D_W: winter	0.044	0.032
D_R: winter	0.274	0.030
NDVI: winter	-0.176	0.165
D_H: urban	-0.259	0.036
D_F: urban	0.440	0.021
D_W: urban	0.279	0.033
D_R: urban	0.889	0.043
NDVI: urban	-0.433	0.124
winter: urban	0.290	0.145
D_H: winter: urban	-0.121	0.043
D_F: winter:urban	0.278	0.060
D_W: winter: urban	0.047	0.041
D_R: winter: urban	-0.148	0.047
NDVI: winter: urban	0.622	0.221

6.4. SUPPLEMENTARY INFORMATION FOR MANUSCRIPT 3

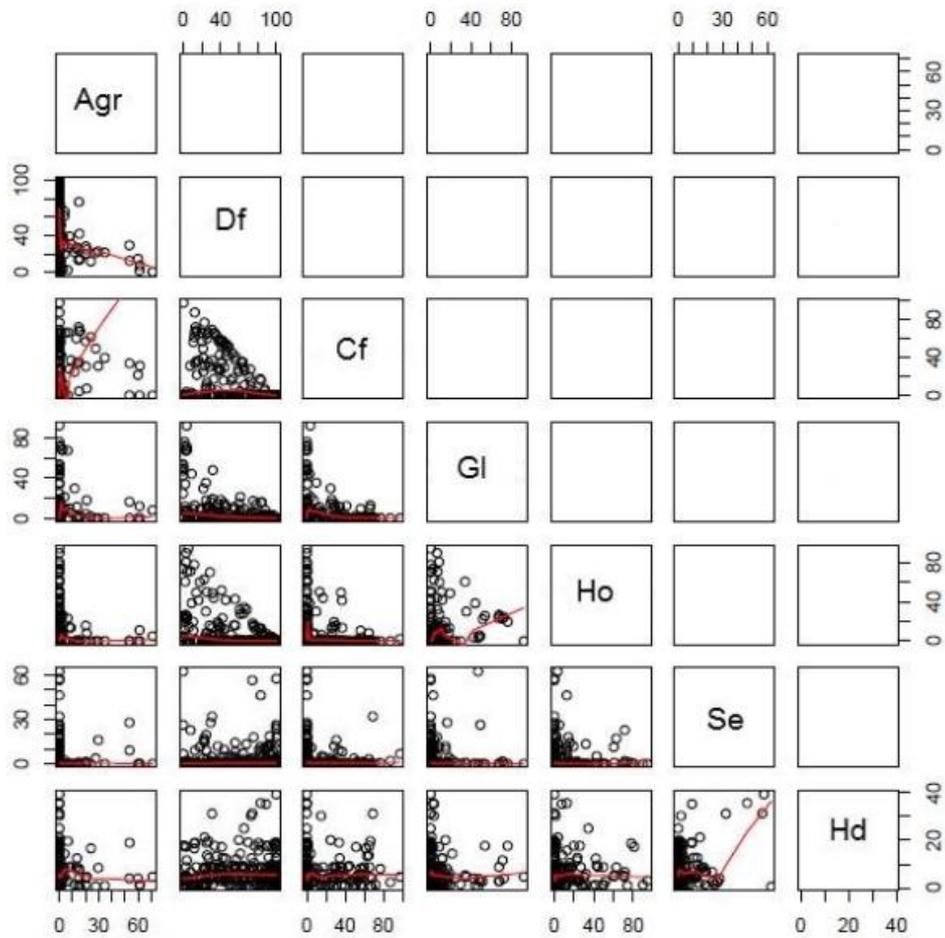
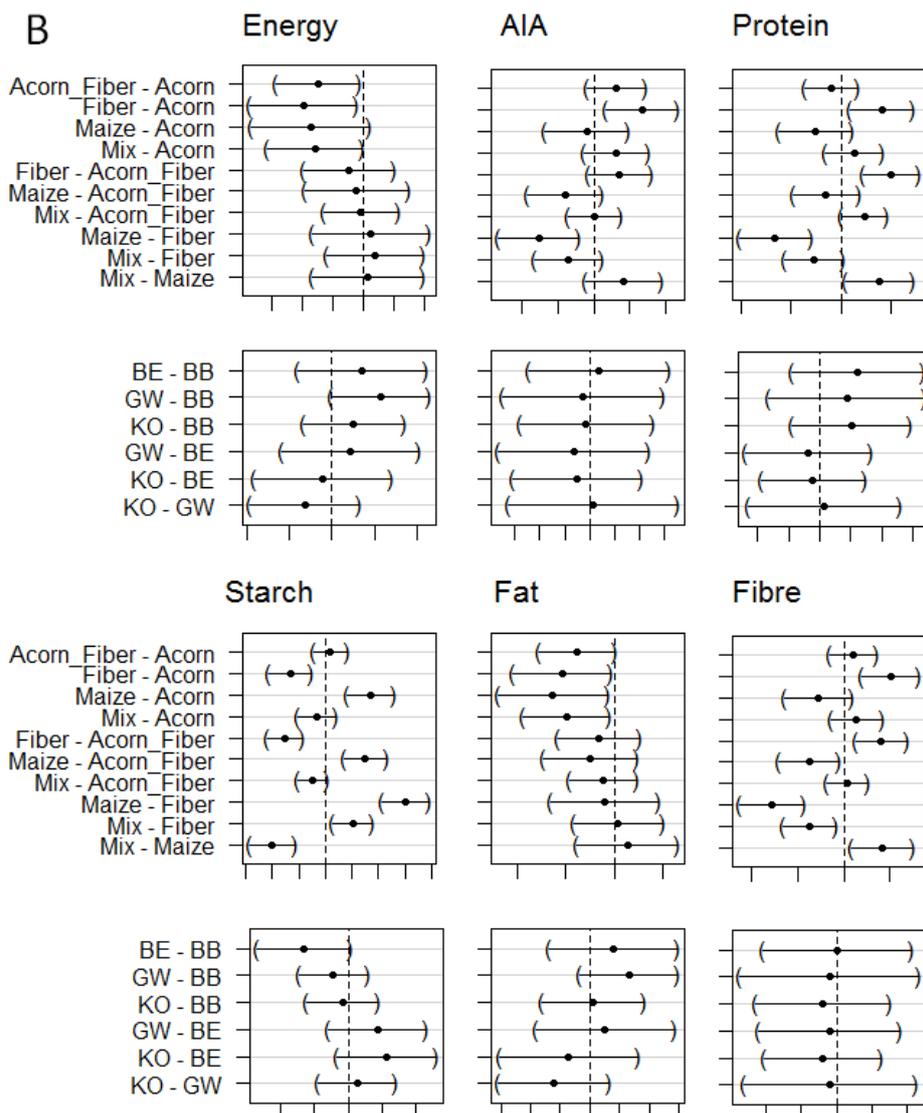
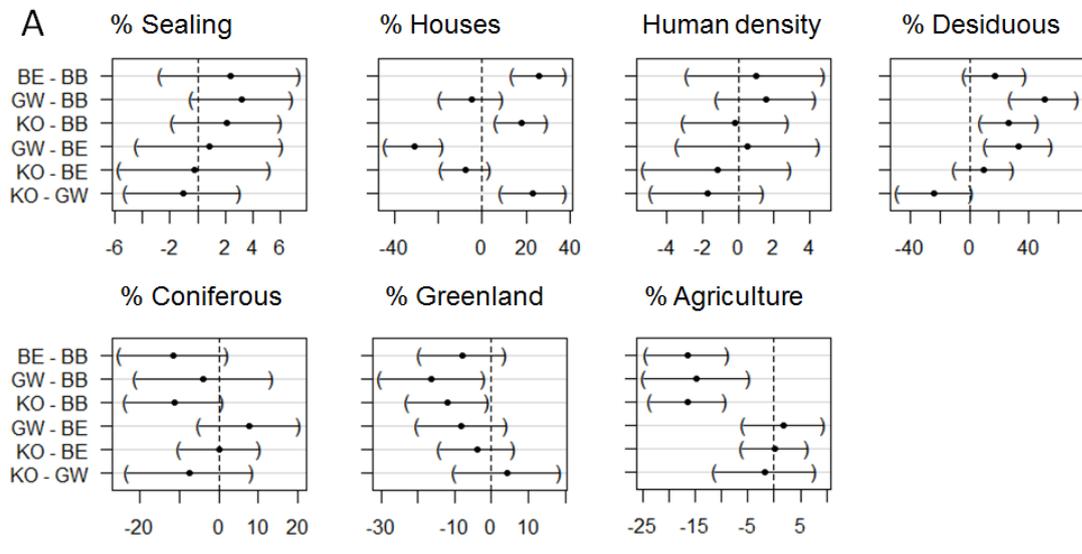


Fig. S1: Correlation plot to test correlation between landscape variables (Pearson’s). Percentage of agriculture (Agr), deciduous forest (Df), coniferous forest (Cf), greenland (GL), houses (Ho), Sealing (Se) and human density (Hd) were used.

Fig. S2: Results of Tukey posthoc test, showing 95% family-wise confidence levels for variable pairs. Significant differences between a pair of levels is given, when the confidence interval does not include 0 (e.g. upper and lower levels both positive or both negative). A) Testing landscape among groups of different origin.



Tab. S1: Macroscopic stomach content analysis for wild boar in Berlin and Brandenburg between 2012 and 2015. Stomach contents of potential anthropogenic origin are listed in total and separated into groups, regarding the different genetic origin of the sampled wild boar. Different groups are the urban forests Grunewald (dark blue, n= 69) Koepenick (yellow, n= 56), Berlin city (white, n=26) and rural Brandenburg (brown, n=96).

Content	Total count	Total %	BB	BE	GW	KO
Apple	5	1.88	3	1		1
Bread	4	1.51				4
Sausage/Cheese	2	0.75				2
Plastic	5	2.26		2	2	1

Tab. S2: Model selection Tab. for testing landscape within groups of different origin.

Model	Intercept	Cluster	df	logLik	AICc	delta	weight
Sealing	2.119	+	7	-881.847	1778.162	0.000	0.966
Sealing_n	3.490		4	-888.357	1784.879	6.717	0.034
House	4.337	+	7	-1024.186	2062.841	0.000	1.000
House_n	9.067		4	-1054.893	2117.950	55.109	0.000
HumDens	6.836	+	7	-817.310	1649.088	0.000	0.820
HumDens_n	7.327		4	-821.975	1652.115	3.027	0.180
Deciduous	67.935	+	7	-1036.087	2086.642	0.000	0.965
Deciduous_n	67.168		4	-1042.551	2093.268	6.626	0.035
Coniferous	67.935	+	7	-1036.087	2086.642	0.000	0.965
Coniferous_n	67.168		4	-1042.551	2093.268	6.626	0.035
Greenland	14.327	+	7	-998.169	2010.807	0.000	1.000
Greenland_n	8.984		4	-1011.363	2030.892	20.084	0.000
Agriculture	13.408	+	7	-875.993	1766.454	0.000	1.000
Agriculture_n	7.848		4	-899.635	1807.435	40.981	0.000

Tab. S3: List of candidate models for linear mixed models, testing the impact of landscape variables on the nutrient composition of wild boar.

Model name	Response	Human variables	Forest variables	Greenland variables	Random
Full	Response	Sealing + Houses + HumanDens	+ Deciduous + Coniferous	+ Greenland + Agriculture	Month + FA
Human1	Response	Sealing + Houses + HumanDens			Month + FA
Human2	Response	Sealing			Month + FA
Human3	Response	Houses			Month + FA
Human1	Response	HumanDens			Month + FA
Forest1	Response		Deciduous + Coniferous		Month + FA
Forest2	Response		Deciduous		Month + FA
Forest3	Response		Coniferous		Month + FA
Green1	Response			Greenland + Agriculture	Month + FA
Green2	Response			Greenland	Month + FA
Green2	Response			Agriculture	Month + FA
null	Response				Month + FA

Tab. S4: Model selection Tab. for linear mixed models, testing the impact of origin and stomach content category on the nutrient composition of wild boar stomachs.

Model	Intercept	Origin	Stomach content category	df	logLik	AICc	delta	weight
<i>Energy</i>								
Full	20.327	+	+	11	-578.736	1180.595	0.000	0.951
Null	19.262			4	-589.173	1186.511	5.917	0.049
<i>MOF</i>								
Null	2.962			4	-195.533	399.232	0.000	1.000
Full	2.816	+	+	11	-201.285	425.693	26.461	0.000
<i>AIA</i>								
Full	5.250	+	+	11	-833.894	1690.912	0.000	1.000
Null	8.231			4	-853.873	1715.912	25.001	0.000
<i>Protein</i>								
Full	16.316	+	+	11	-726.563	1476.249	0.000	1.000
Null	17.496			4	-752.729	1513.623	37.375	0.000
<i>Starch</i>								
Full	25.785	+	+	11	-947.003	1917.129	0.000	1.000
Null	24.057			4	-999.733	2007.632	90.503	0.000
<i>Fat</i>								
Full	12.417	+	+	11	-833.811	1690.745	0.000	1.000
Null	8.731			4	-851.902	1711.970	21.225	0.000
<i>Fibre</i>								
Full	8.084	+	+	11	-723.097	1469.318	0.000	1.000
Null	9.338			4	-750.381	1508.928	39.610	0.000

Tab. S 5: FULL Model selection Tab. for linear mixed models, testing nutrient values and food quality in stomachs of wild boar from Berlin and Brandenburg between 2012 and 2015. For different response variables, the energy amount of each stomach (Energy_BB= Energy within stomachs of wild boar from Brandenburg, Energy_BE= wild boar from Berlin city, Energy_GW= wild boar from the Grunewald forest, Energy_KO=wild boar from the Koepenick forest) content was measured in KJ/g dry matter. The modulus of fines (MOF) was calculated after particle size determination; the acid insoluble ash (AIA) is given in percent, such as amount of protein, starch, fat and fibre.

The explanatory variables describe the landscape within a buffer around each sample location and were grouped regarding their expected influence: Sealing (percentage of sealed surface), houses (percentage of houses) and HumDens (Human density per km²) are human associated landscape variables and shaded in grey. The Models, which include only these variables, are called “Hum1”-“Hum4”. Deciduous (percentage of deciduous forest and Coniferous (percentage of coniferous forest) are forest associated landscape variables (shaded in green); the models which include only these variables are called “For1”-“For3”. Greenland (percentage of greenland) and Agriculture (percentage of agriculture) are field associated landscape variables (shaded in yellow); the model which include only these variables are called “Agr1”-“Agr3”. A model which contains all landscape variables is called “LS”, the intercept only model is called “null”.

The degree of freedom is abbreviated as “df”, the logarithmic likelihood is abbreviated as “logLik”. Akaike’s information criterion corrected for small sample size (AICc) is used for model selection, such as the Bayesian information criterion (BIC). The delta shows the difference between the AICc values.

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Model	Intercept	Sealing	houses	Hum Dens	Deciduous	Coniferous	Greenland	Agriculture	df	logLik	AICc	delta
Energy_BB												
null	19.117								4	-237.15	482.73	0.00
Hum2	18.949	0.130							5	-236.35	483.36	0.63
Hum3	19.573		-0.051						5	-238.36	487.38	4.65
Agr3	18.938							0.032	5	-239.13	488.94	6.20
Hum4	19.170			-0.022					5	-239.16	488.99	6.25
Agr2	19.601						-0.024		5	-239.32	489.30	6.56
For1	19.168					-0.007			5	-240.50	491.66	8.93
Hum1	19.614	0.145	-0.041	-0.064					7	-239.23	493.73	10.99
Agr1	19.319						-0.022	0.029	6	-241.41	495.76	13.02
LS	19.815	0.131	-0.034	-0.052		-0.009	-0.013	0.013	10	-248.04	518.67	35.93
Energy_BE												
Agr3	19.828							-9.036	5	-55.13	123.26	0.00
For1	19.676					1.210			5	-56.23	125.46	2.20
null	19.698								4	-58.83	127.57	4.31
Agr1	19.710						0.014	-8.476	6	-57.25	130.93	7.67
Hum4	19.493			0.027					5	-60.71	134.41	11.15
Agr2	19.553						0.018		5	-60.95	134.89	11.63
Hum2	19.725	-0.006							5	-60.97	134.94	11.68
Hum3	19.775		-0.003						5	-61.86	136.73	13.47
Hum1	19.470	-0.035	-0.001	0.053					7	-65.48	151.18	27.92
LS	19.429	-0.034	-0.002	0.054		1.413	0.015	-7.985	10	-61.11	156.88	33.62
Energy_GW												
null	20.181								4	-162.22	333.06	0.00
For1	22.972				-0.036				5	-161.90	334.76	1.70
Hum3	20.132		0.238						5	-162.21	335.38	2.32
Agr1	20.198						0.047		5	-163.86	338.67	5.61
Hum4	20.349			-0.016					5	-164.38	339.71	6.65
Hum2	20.153	0.005							5	-164.82	340.59	7.53
Hum1	20.304	0.013	0.238	-0.024					7	-166.79	349.43	16.36
LS	20.323	0.013	0.141	-0.022			0.031		8	-168.50	355.41	22.35
Energy_KO												
null	19.268								4	-120.25	249.29	0.00
For3	19.210					0.070			5	-121.40	253.99	4.70
Agr1	19.756						-0.043		5	-121.44	254.07	4.78
Hum4	19.090			0.028					5	-122.30	255.80	6.51
Hum2	19.273	0.001							5	-123.00	257.20	7.91
Hum3	19.190		0.003						5	-123.82	258.85	9.56
For2	19.110				0.003				5	-124.13	259.46	10.17
For1	18.886				0.006	0.096			6	-125.11	263.94	14.65
Hum1	19.015	0.003	0.003	0.028					7	-128.59	273.52	24.23
LS	22.205	0.028	-0.027	0.032	-0.029	0.090	-0.106		10	-132.17	289.24	39.95
MOF												
null	2.96								4	-195.53	399.23	0.00
Hum4	2.89			0.009					5	-198.14	406.52	7.29
For3	3.03					-0.004			5	-198.78	407.81	8.58
Agr2	2.94						0.004		5	-199.47	409.19	9.96
Hum3	2.93		0.003						5	-199.80	409.86	10.62
Agr3	2.98							-0.003	5	-199.87	409.99	10.76
Hum2	2.97	-0.002							5	-200.06	410.38	11.14
For2	2.94				0.000				5	-201.39	413.03	13.80
Agr1	2.95						0.004	-0.003	6	-203.82	419.99	20.76
For1	3.05				0.000	-0.004			6	-204.62	421.59	22.36
Hum1	2.87	-0.004	0.003	0.011					7	-206.41	427.30	28.06
Full	2.76	-0.005	0.004	0.011	0.002	-0.002	0.005	0.000	11	-223.83	470.78	71.55
AIA												
null	8.23								4	-853.87	1715.91	0.00
Agr3	8.82							-0.113	5	-853.96	1718.17	2.25
Hum4	7.93			0.043					5	-855.41	1721.07	5.16
Hum2	8.34	-0.032							5	-855.69	1721.62	5.71

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Agr2	7.97						0.034		5	-855.86	1721.97	6.06
For3	7.91					0.020			5	-856.36	1722.97	7.06
Hum3	8.12		0.013						5	-856.43	1723.10	7.19
Agr1	8.54						0.036	-0.114	6	-855.89	1724.12	8.21
For2	8.35				-0.002				5	-857.08	1724.40	8.49
For1	7.99				-0.001	0.019			6	-859.55	1731.44	15.53
Hum1	7.84	-0.045	0.012	0.061					7	-859.58	1733.64	17.73
LS	7.39	-0.038	0.014	0.051	0.009	0.012	0.047	-0.099	11	-866.88	1756.88	40.96
Protein												
For3	18.81					-0.062			5	-751.45	1513.14	0.00
null	17.50								4	-752.73	1513.62	0.48
Agr3	17.80							-0.060	5	-753.69	1517.64	4.50
Hum4	17.46			0.005					5	-754.86	1519.98	6.84
Hum2	17.55	-0.023							5	-754.94	1520.13	6.99
Agr2	17.42						0.012		5	-755.47	1521.19	8.05
Hum3	17.52		-0.003						5	-755.79	1521.83	8.69
For1	18.97				-0.003	-0.063			6	-755.02	1522.40	9.26
For2	17.45				0.001				5	-756.33	1522.92	9.78
Agr1	17.73						0.012	-0.060	6	-756.44	1525.24	12.10
Hum1	17.48	-0.026	-0.003	0.015					7	-760.04	1534.55	21.41
LS	23.11	-0.035	-0.056	0.021	-0.045	-0.104	-0.052	-0.108	11	-762.12	1547.37	34.23
Starch												
Agr3	23.51							0.206	5	-998.37	2007.00	0.00
null	24.06								4	-999.73	2007.63	0.64
For3	21.05					0.133			5	-999.07	2008.38	1.39
Agr1	24.26						-0.120	0.205	6	-998.19	2008.73	1.73
Agr2	24.85						-0.127		5	-999.41	2009.07	2.07
Hum4	24.91			-0.131					5	-1000.35	2010.96	3.96
Hum2	24.04	0.006							5	-1001.12	2012.48	5.49
For1	18.64				0.044	0.146			6	-1000.55	2013.46	6.46
Hum3	24.31		-0.027						5	-1001.65	2013.55	6.56
For2	22.53				0.029				5	-1001.89	2014.02	7.03
Hum1	25.13	0.040	-0.027	-0.148					7	-1003.54	2021.54	14.55
LS	14.42	0.073	0.109	-0.149	0.114	0.162	0.003	0.280	11	-1002.72	2028.56	21.56
Fat												
null	8.73								4	-851.90	1711.97	0.00
Agr2	9.33							-0.066	5	-852.39	1715.02	3.05
Hum4	7.94			0.111					5	-852.43	1715.11	3.14
Hum2	8.47	0.077							5	-852.94	1716.12	4.15
Agr3	8.49							0.029	5	-853.83	1717.90	5.93
Hum3	8.91		-0.016						5	-854.40	1719.05	7.09
For3	8.67					0.002			5	-854.57	1719.38	7.41
For2	8.73				0.000				5	-855.14	1720.54	8.57
Agr1	9.11							-0.066	6	-854.35	1721.06	9.09
Hum1	8.06	0.056	-0.014	0.089					7	-856.43	1727.33	15.36
For1	8.69				0.000	0.002			6	-857.76	1727.86	15.89
LS	13.50	0.049	-0.061	0.095	-0.056	-0.070	-0.125	-0.032	11	-862.25	1747.63	35.66
Fibre												
null	9.34								4	-750.38	1508.93	0.00
Agr2	9.09							0.038	5	-751.77	1513.78	4.85
Hum4	9.28			0.009					5	-752.51	1515.27	6.34
For3	9.93					-0.027			5	-752.56	1515.37	6.45
Agr3	9.41							-0.014	5	-752.75	1515.74	6.81
Hum2	9.31	0.010							5	-752.76	1515.77	6.85
Hum3	9.30		0.006						5	-753.42	1517.09	8.16
For2	9.82				-0.010				5	-753.56	1517.36	8.44
Agr1	9.16							0.038	6	-754.14	1520.63	11.70
For1	10.56				-0.012	-0.030			6	-755.55	1523.46	14.53
Hum1	9.23	0.008	0.006	0.006					7	-757.89	1530.24	21.32
LS	10.76	0.001	-0.016	0.014	-0.015	-0.029	0.017	-0.029	11	-767.00	1557.11	48.19

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Selbständigkeitserklärung

Hiermit versichere ich, dass ich die vorliegende Doktorarbeit eigenständig verfasst und keine anderen als die angegebenen Quellen und Hilfsmittel verwendet habe

Berlin, 30.11.2016

Milena Stillfried