Universitat Autònoma de Barcelona

THE SYNURBIZATION OF WILD BOAR
IN THE CITY OF BARCELONA, SPAIN

Carlos González Crespo

THE SYNURBIZATION OF WILD BOAR IN THE CITY OF BARCELONA, SPAIN

Autor

Carlos González Crespo

Director

Dr. Santiago Lavín González

Director y tutor

Dr. Jorge Ramón López Olvera

Tesis doctoral

Programa de Doctorat en Biodiversitat

Departament de Biologia Animal, Biologia Vegetal i Ecologia

Facultat de Biociències

Universitat Autònoma de Barcelona

2020

Els doctors Jorge Ramón López Olvera, Professor Titular d'Universitat, i Santiago Lavín González, Catedràtic d'Universitat, del Departament de Medicina i Cirurgia Animals de la Universitat Autònoma de Barcelona,

Informen:

Que la memoria titulada **"The synurbization of the wild boar in the city of Barcelona, Spain"**, presentada per **Carlos González Crespo** para a la obtención del grado de Doctor en Biodiversidad por la Universitat Autònoma de Barcelona, se ha realizado sobre nuestra dirección y, una vez considerada satisfactoriamente finalizada, autorizamos su presentación para que sea avaluada por la comisión correspondiente.

Y para que así conste a los efectos oportunos, firmamos el presente informe en Bellaterra, a 19 de noviembre de 2020.

Jorge Ramón López Olvera	Santiago Lavín González
Director i tutor	Director

Carlos González Crespo
Doctorando

ACKNOWLEDGEMENTS, AGRADECIMIENTOS, AGRAÏMENTS

'They say “**well science doesn't know everything”.**
Well science knows it doesn't know everything; otherwise it would stop.'
- Dara Ó Briain-

Escribir esta parte de la tesis debería ser la más sencilla, sin embargo, después de cuatro años de tanto esfuerzo, en los que me he cruzado con tanta gente increíble, no sé cómo empezar a agradecer a todos aquellos que han hecho posible esta tesis.

Mi primer agradecimiento es para Santiago, que gracias a sus consejos llegué a Barcelona a hacer un Master y aquí estamos seis años después aprendiendo cada día. Gracias de verdad por devolverme al mundo animal, por pensar en mí para el proyecto de las palomas del que tantas cosas he aprendido sobre la naturaleza humana, por el marisco, las raquetas, las truchas y las cenas en Solle.

También a Jorge (5), mi guía en el proceso doctoral (5) y con el que tan buen rollo he tenido desde el TFM (5), por tu buen humor (5) y apoyo (5). A Emmanuel mi sensei de la estadística, que me enseño que los árboles también se pueden podar con el R y aplicar los principios de la esgrima a la vida, “ante la fuerza, debilidad”. A Gregorio y Roser, por los buenos viajes a los congresos y por enseñarme que en los verdaderos científicos no hay vanidad.

A Carles, sin ti estos años no hubieran sido igual, desde el principio conectamos a un nivel muy molón, eres una persona increíble. Siempre nos quedaran nuestros cafés en el parking. A Raquel, nuestro sargento estelar, organizadora esencial en el mar de caos que somos. A Johan y Marta por ser tan grandes, y hacer que ir al despacho siempre fuera un placer. A Genis por que donde estás, el ambiente siempre es mejor, y Omar, grande en todos los sentidos, llevas en tu interior todo el superpower del Heavy. A todos los sefitos que han pasado durante estos años, en especial Arian, Xavi, Andreu y Diana.

A Beatriz, por tu disponibilidad para todo, acogerme en California, hacerme sentir como en casa y enseñarme tanto tanto en solo tres meses. Y por ese conciertazo de ZZTop.

Al equipo del Port d'Informació Científica, en especial a Vanessa y Carles por que sin su ayuda no hubiera podido usar el super-mega-ordenador, siempre dispuestos a resolver mis dudas. Me habéis ayudado mas de lo que os podeis imaginar.

Un agradecimiento especial a Carme Maté, por su simpatía y rigor científico a la hora de gestionar la fauna urbana de Barcelona y a Chema Lopez, por ser sin saberlo, el que

me encaminó a meterme en el mundo de los modelos del que he acabado haciendo la presente tesis.
Quiero agradecer a F. Llimona, F. Calomardo y M.Martí, por su colaboración y disposición para obtener y compartir los datos biológicos de la población de jabalíes del CNP. También estoy en deuda con el Ajuntament de Barcelona, Agents Rurals y Guàrdia Urbana de Barcelona, quienes apoyaron y colaboraron en todo lo necesario para la realización de esta tesis.

A mi padre, que quien iba a decirme cuando de niño escuchaba las historias de los cazadores en Salamón, que acabaría haciendo un doctorado sobre jabalíes y simulaciones. A mis abuelos Gloria y Ovidio, con quienes pasé mis veranos en los picos de Europa, donde conocí el lobo, el rebeco, el corzo, el venado, las águilas, la caraviella, la trucha, el desmán y la nutria.
A mi madre, por ser mi apoyo y guía desde siempre y por enseñarme el amor a la lectura que me ha llevado hasta aquí. A mis abuelos Sixta y Martiniano, por enseñarme la vida sencilla e increíble, llena de colores y sabores, del agricultor y pastor, a entender la naturaleza y como se debe convivir con ella, os echo mucho de menos. Por ese quebrantahuesos que me enseñaste con 5 años, y que en teoría no debería estar ahí, pero estaba. Y por supuesto por enseñarme a cómo hacer y tirar con la honda a la manera de los pastores. A mis tíos Carlos y Belen y mis primos Raul y Javier, sois mi infancia.

A mi Águeda, mi hermana pequeña, ya no tan pequeña, desde hace 32 años compartimos y nos apoyamos, llegaras a ser la mejor enfermera del mundo.

Y a Nora, mi tifón particular, compañera de mi vida. Que me has tenido que aguantar estos cuatro años de locura, que me das tanto, aunque a veces no lo merezca. Por tu sonrisa y tu energía, a partir de ahora empieza una nueva aventura en nuestra vida.

TABLE OF CONTENTS

1. SUMMARY

1.1 SUMMARY

Synurbic species respond to global urbanization by gradually colonizing cities and using urban environments, where social and ecological factors drive close human-wildlife interactions. The lack of management in the human-wildlife interactions leads to conflicts which generate changes in animal population dynamics and an increase in public and private expenses. The population densities of wild boar (WB, *Sus scrofa*) are increasing globally thanks to its great adaptability and plastic behavior, WB is spreading into (peri)urban areas. In these areas, WB presence is associated to new close human-WB interactions, which generate an increasing concern regarding the epidemiological risk for public health and other associated conflicts. Synurbization favored by the availability of anthropogenic food resources, increases aggregation and intraspecific tolerance, enhancing the contact rates of synurbic WB and citizens, with the consequent risk of pathogen transmission. This thesis provides insights into the drivers of WB dynamics in the Collserola Natural Park (CNP), and the most effective management strategies to reduce WB population density. Furthermore, through the development of an agent-based model, the social-ecological system driving the use of the urban ecosystem by synurbic WB and the human- WB interactions in the (peri)urban area of Barcelona are analysed. Finally, the epidemiological risk posed by WB in the (peri)urban area of Barcelona is evaluated, quantifying and spatially locating their role in the maintenance, circulation and spatial spread of pathogens.

The results revealed that, under the current conditions, the CNP WB population will continue to increase. The most efficient strategy to reduce WB abundance was a combination of reducing supplementary anthropogenic food resources and selective removal of WB under two years of age. The agent-based model developed, obtained high accuracy to predict the magnitude and location of WB movements as compared to reports of WB observations in the city of Barcelona. The model predicted 115 attack events and 1442 direct feeding events during one year of simulation. The good performance of the model reflects the value of this prototype as predictive model to detect priority areas of human-WB interactions and conflicts.

This thesis also describes an epidemiological expansion of agent-based model, to test different epidemiological scenarios that could be used in the evaluation of risk for public health, and support decision-making, of three relevant pathogens at risk of transmission at the wild-domestic-human interface: hepatitis E virus (HEV), antimicrobial resistant *Campylobacter* (AR-CB) and African swine fever virus (ASFV).

In the ASFV scenario, the entire WB population was exposed to the virus 51 to 71 days after the index case. ASFV transmission was mediated by carcasses in 87.6% of the cases and by direct contact in the remaining 12.6%. The outbreak lasted between 71 and 124 days, reducing 95% of the initial population. Model outputs of citizen exposition for HEV and AR-CB (according to the model, 457and 462 humans would have contacted the pathogen, respectively) were in agreement with the World Health Organization estimations (480 for HEV and 264 to 558for AR-CB) for the modelled human population in the estimated time extent. Despite the difference in the prevalence of pathogens (20% and 60% for HEV and AR-CB, respectively) in the WB population, the similar number of exposed citizens in each pathogen scenario, suggest the major role of feces in the transmission of these pathogens, resulting consequently in a significant risk to public health.

The models developed could be useful also to assess the efficacy, efficiency and cost-effectiveness of potential management strategies, as well as to evaluate the spread, transmission risks, and epidemiological implications for the WB population and for public health of different WB pathogens.

1.2 RESUMEN

Las especies sinúrbicas responden a la urbanización global colonizando gradualmente las ciudades y utilizando entornos urbanos, donde los factores sociales y ecológicos influyen en las interacciones entre humanos y vida silvestre. La falta de gestión en las interacciones entre humanos y fauna salvaje conduce a conflictos que generan cambios en la dinámica de la población animal y un aumento de los gastos públicos y privados. Las densidades poblacionales de jabalí (*Sus scrofa*) están aumentando globalmente, y gracias a su gran adaptabilidad y comportamiento plástico se está extendiendo hacia áreas (peri)urbanas. En estas áreas se asocia a nuevas interacciones entre humanos y jabalíes, que generan una creciente preocupación por el riesgo epidemiológico para la salud pública y otros conflictos asociados. La sinurbización, favorecida por la disponibilidad de recursos alimentarios antropogénicos, aumenta la agregación y la tolerancia intraespecífica, incrementando las tasas de contacto del jabalí sinúrbico y los ciudadanos, con el consiguiente riesgo de transmisión de patógenos. Esta tesis proporciona información sobre los factores que influyen en la dinámica del jabalí en el Parque Natural de Collserola (PNC) y las estrategias de gestión más efectivas para reducir la densidad de las poblaciones de jabalí. Además, a través del desarrollo de un modelo basado en agentes, se analiza el sistema socio-ecológico que rige el uso del ecosistema urbano por el jabalí sinúrbico y las interacciones entre humanos y jabalíes en el área (peri)urbana de Barcelona. Finalmente, se evalúa el riesgo epidemiológico que supone el jabalí en el área (peri)urbana de Barcelona, cuantificando y localizando espacialmente su papel en el mantenimiento, la circulación y la diseminación espacial de patógenos.

Los resultados revelaron que, en las condiciones actuales, la población de jabalí del PNC seguirá aumentando. La estrategia más eficiente para reducir la abundancia de jabalí fue una combinación de la reducción de los recursos alimenticios antropogénicos suplementarios y la eliminación selectiva de jabalíes menores de dos años. El modelo basado en agentes desarrollado obtuvo una alta precisión para predecir la magnitud y ubicación de los movimientos del jabalí en comparación con los informes de observaciones de jabalí en la ciudad de Barcelona. El modelo predijo 115 eventos de ataque y 1442 eventos de alimentación directa durante un año de simulación. El buen desempeño del modelo refleja el valor de este prototipo como modelo predictivo para detectar áreas prioritarias de interacciones y conflictos entre humanos y jabalíes.

Esta tesis también describe una expansión epidemiológica del modelo basado en agentes, con el objetivo de evaluar diferentes escenarios epidemiológicos que podrían ser utilizados en la evaluación del riesgo para la salud pública, y respaldar la toma de decisiones, de tres patógenos relevantes en riesgo de transmisión en la interfaz entre animales salvajes, animales domésticos y humanos: el virus de la hepatitis E (VHE), *Campylobacter* resistente a antimicrobianos (CB-RA) y el virus de la peste porcina africana (PPA).

En el escenario de PPA, toda la población de jabalí estuvo expuesta al virus de 51 a 71 días después del caso índice. La transmisión del virus de la PPA estuvo mediada por los cadáveres en el 87,6% de los casos y por contacto directo en el 12,6% restante. El brote duró entre 71 y 124 días, reduciendo la población inicial en un 95%. Los resultados del modelo de exposición ciudadana para VHE y CB-RA (según el modelo, 457 y 462 humanos habrían contactado con el patógeno, respectivamente) coincidieron con las estimaciones de la Organización Mundial de la Salud (480 para HEV y entre 264 y 558 para CB-RA) para la población humana modelizada en la extensión de tiempo estimada. A pesar de la diferencia en la prevalencia de patógenos (20% y 60% para HEV y CB-RA, respectivamente) en la población de jabalí, el número similar de ciudadanos expuestos en cada escenario de patógenos sugiere el papel principal de las heces en la transmisión de estos. patógenos, lo que resulta en un riesgo significante para la salud pública.

Los modelos desarrollados podrían ser útiles también para evaluar la eficacia, la eficiencia y la rentabilidad de posibles estrategias de gestión, así como para evaluar la propagación, los riesgos de transmisión y las implicaciones epidemiológicas para la población de jabalí y para la salud pública de diferentes patógenos del jabalí.

1.3 RESUM

Les espècies sinúrbiques responen a la urbanització global colonitzant gradualment les ciutats i utilitzant entorns urbans, on els factors socials i ecològics influeixen en les interaccions entre humans i vida salvatge. La falta de gestió en les interaccions entre humans i fauna salvatge condueix a conflictes que generen canvis en la dinàmica de la població animal i un augment de les despeses públiques i privades. Les poblacions de porc senglar (*Sus scrofa*) estan augmentant globalment, i gràcies a la seva gran adaptabilitat i al seu comportament plàstic s'està estenent cap a àrees (peri)urbanes on s'associa a noves interaccions entre humans i senglars. Aquestes noves interaccions generen una preocupació creixent pel risc epidemiològic per a la salut pública i altres conflictes associats. La sinurbització, afavorida per la disponibilitat de recursos alimentaris antropogènics, augmenta l'agregació i la tolerància intraespecífica, incrementant les taxes de contacte del senglar sinúrbic i els ciutadans, amb el conseqüent risc de transmissió de patògens. Aquesta tesi proporciona informació sobre els factors que influencien la dinàmica del porc senglar al Parc Natural de Collserola (PNC) i les estratègies de gestió més efectives per a reduir la densitat de les poblacions de senglars. A més, a través del desenvolupament d'un model basat en agents, s'analitza el sistema socio-ecològic que regeix l'ús de l'ecosistema urbà pel senglar sinúrbic i les interaccions entre humans i senglars en l'àrea (peri)urbana de Barcelona. Finalment, s'avalua el risc epidemiològic que suposa el senglar en l'àrea (peri)urbana de Barcelona, quantificant i localitzant espacialment el seu paper en el manteniment, la circulació i la disseminació espacial de patògens.

Els resultats varen revelar que, en les condicions actuals, la població de senglar del PNC seguirà augmentant. L'estratègia més eficient per a reduir l'abundància de senglar va ser una combinació de reducció dels recursos alimentaris antropogènics suplementaris i l'eliminació selectiva de senglars menors de dos anys. El model basat en agents desenvolupat va obtenir una alta precisió per a predir la magnitud i la ubicació dels moviments del senglar en comparació amb els informes d'observacions de senglar a la ciutat de Barcelona. El modelo va predir 115 episodis d'atac i 1442 episodis d'alimentació directa durant un any de simulació. El bon acompliment del model reflecteix el valor d'aquest prototipus com model predictiu per a detectar àrees prioritàries d'interaccions i conflictes entre humans i senglars.

Aquesta tesi també descriu una expansió epidemiològica del modelo basat en agents, amb l'objectiu d'avaluar diferents escenaris epidemiològics que podrien ser utilitzats en l'avaluació del risc per a la salut pública, i donar suport a la presa de decisions, de tres patògens rellevants a la interfície entre animals salvatges, animals domèstics i humans: el virus de l'hepatitis E (VHE), *Campylobacter* resistent a antimicrobians (CB-RA) i el virus de la pesta porcina africana (PPA).

En l'escenari de PPA, tota la població de senglar va estar exposada al virus de 51 a 71 dies després del cas índex. La transmissió del virus de la PPA va estar determinada pels cadàvers en el 87,6% dels casos i per contacto directe en el 12,6% restant. El brot va durar entre 71 i 124 dies, reduint la població inicial en un 95%. Els resultats del model d'exposició ciutadana per al VHE i CB-RA (segons el model, 457 i 462 humans haurien contactat amb el patogen, respectivament) varen coincidir amb les estimacions de l'Organització Mundial de la Salut (480 per a HEV i entre 264 i 558 per a CB-RA) per a la població humana modelitzada en l'extensió de temps estimada. A pesar de la diferència en la prevalença de patògens (20% i 60% per a HEV i CB-RA, respectivament) a la població de seglar, el número similar de ciutadans exposats en cada escenari de patògens suggereix un paper determinant de les femtes en la transmissió d'aquests patògens, el que resulta en un risc significant per a la salut pública.

Els models desenvolupats podrien ser útils també per a avaluar l'eficàcia, l'eficiència i la rendibilitat de possibles estratègies de gestió, així com per a avaluar la propagació, els riscs de transmissió i les implicacions epidemiològiques per a la població de senglars i per a la salut pública de diferents patògens del senglar.

2. INTRODUCTION

2.1. The urban ecosystem

The term *Urban*, in the context of the present thesis, refer to major cities and dense settlements of >100 persons/km, including both the sprawling edges of the major cities (metropolitan areas), and small towns.

2.1.1. Global urban sprawl

Since the XIXth century, humanity is experiencing a social revolution as a result of urbanization, the spatial phenomenon of concentration of human population living and working in central areas (Mcdonal et al., 2011). The rural exodus started as a consequence of mechanization in the industrial revolution and increased after the II World War, and it is considered as the greatest human-environmental experiment of all time (Meyerson et al., 2007). The percentage of urban inhabitants represented just 10% of the global population in 1900, and has increased with urbanization expansion to currently reach 56% of the world human population. This trend will continue in the next years. More than 95% of the global population increase will be in cities of the developing world, by 2050 will come and up to 68.4% worldwide and close to the 80% in the most industrialized nations (UNPD 2018 (Grimm et al., 2008)). Additionally, some cities are growing until reaching unprecedented dimensions in the history of humanity, the new megacities (>10 million, by convention) (Grimm et al., 2008). But in regions where of economy is declining, a divergent trend has been observed. Here the phenomenon of shrinking cities is associated with an enhanced emergence of “wild” ecosystems in urban-industrial areas demonstrating the ecological potential of urban regions (Kowarik, 2011, 2018).

Although urban population growth has occurred on less than 3% of the global terrestrial surface, the impact has been global, with 78% of carbon emissions, 60% of residential water use, and 76% of wood used for industrial purposes attributed to cities (Brown, 2001;Grimm et al., 2008). As the limits of the city expand into surrounding rural landscapes, these peri-urban environments link cities in extended urbanized regions (Grimm et al 2008). New trends suggest that rather than independent entities, cities aggregate in a limited number of dominant megapolitan regions across the globe, as coalitions of urban centers and increasingly built-up intervening regions (Brown, 2001; Grimm et al., 2008). The next frontier in urban ecology is to understand urbanization in the context of biophysical, economic, or political settings based on this megapolitan concept (Grimm et al., 2008).

2.1.2. Rise of urban ecology

Urban areas have been out of the scope of ecological studies for most of the 20th century, resulting in little contribution from ecological knowledge to solving urban environmental issues (Grimm et al., 2008).

2.1.2.1. The imbalance of nature

Ecology traditionally assumed that nature maintains a state of stability where natural disturbances, as well as human actions, have little or no long-term influence. Thus, humans were treated as an external agent to the systems, rather than part of the ecosystem. Under the new non-equilibrium paradigm involving physical, ecological, and social sciences, ecosystems are not an end-point but open systems driven by processes, potentially regulated by external forces, where humans are components (Alberti, 2008; Mcdonal et al., 2011; McDonnell & Niemelä, 2011).

2.1.2.2. The ubiquitous human footprint

After the publication of the rising atmospheric CO2 data in the early 1960s ecologists recognized the impact of humans, by changing our global climate, as force of nature capable of modifying ecosystems, (McDonnell & Niemelä, 2011), with no ecosystem on Earth free from the actions of humans (Vitousek et al., 2008).

It is now widely accepted that (1) humans have such profound effects on natural ecosystems that they can be correctly labeled as a *keystone species* (Niemelä et al., 2013); (2) human actions have altered at global scales the distribution of organisms and flux of energy and matter; and (3) the growth and expansion of cities are major drivers in local, regional, and global environmental change (McDonnell & Niemelä, 2011)

Nowadays, ecosystems are considered to be the product of human–nature interaction (Mann, 2006). On the other hand, due to the plasticity behavior of the species, humans have adapted their culture to the specific challenges and opportunities of their environments (Strohbach et al., 2014). The mutual interaction and adaptation between the social and natural components of the system are defined as coupled human and natural systems (CHANS) (Strohbach et al., 2014). CHANS create significant ecological patterns known as Anthromes, Anthropogenic Biomes, or Human Biomes, which are formed by global patterns in human populations and their uses of land over the long-term(Ellis, 2011; Ellis & Ramankutty, 2008). Depending of population density 18 anthropogenic biomes are categorized into five categories, namely dense settlement, village, cropland, rangeland and forested (seminatural) anthromes, occupying 75% of Earth's ice-free land, and the remaining 25% categorized as wildlands, with no evidence of human alteration(Ellis, 2011; Ellis & Ramankutty, 2008).

2.1.2.3. Legitimation of urban ecosystems

The Man and Biosphere (M&B) program of the United Nations Educational, Scientific and Cultural Organization (United Nations Educational, Scientific and Cultural Organization, 2020), initiated to conserve and study both natural and cultural ecosystems, consolidated the emerging discipline of urban ecology (McDonnell & Niemelä, 2011). This program was critical to establish the first multidisciplinary ecological studies of human settlements, integrating basic and applied natural and social science research to explore and elucidate the multiple dimensions of urban ecosystems (McDonnell & Niemelä, 2011). As a result, multidisciplinary research involving ecologists and scientists from other areas, as well as managers and engineers, is increasing to understand and manage growing urban ecosystems (Grimm et al., 2008).

Urban ecology studies the patterns and processes of urban ecosystems integrating the theory and methods of both natural and social sciences (Grimm et al., 2008). Urban areas are heterogeneous, dynamic landscapes and complex, adaptive, social-ecological systems (SES) (Grimm et al., 2008; Lischka et al., 2018; Virapongse et al., 2016). These SES are systems of biophysical and social factors interacting at multiple spatial, temporal, and organizational scales, where interactions among ecosystems, biodiversity and people take place (Figure 2.1, (Lischka et al., 2018; Virapongse et al., 2016)).To understand urban wildlife ecology, interactions and feedback between social and natural systems must therefore be considered (Strohbach et al., 2014), measuring ecological variables (e.g., diversity, landscape pattern), social variables (e.g., economics, social networks, values), and variables that link social and natural systems (e.g., anthropogenic landscape change, natural resource use, and waste disposal (Strohbach et al., 2014).

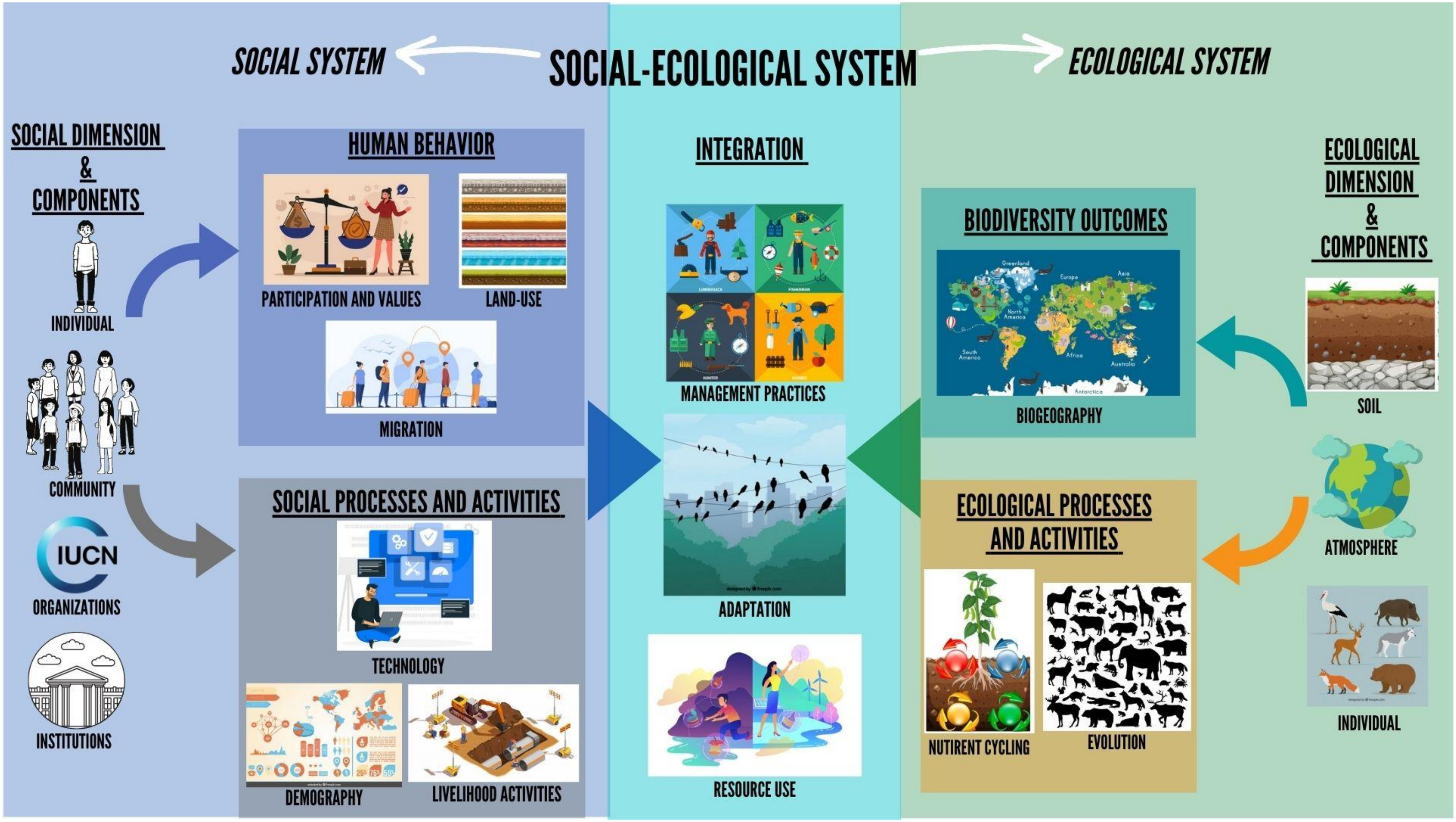


Figure 2.1. Representation of the social-ecological systems (SES). Adapted from (Gardner et al., 2013; Lischka et al., 2018; Virapongse et al., 2016).

2.1.3. Urbanization as architect of the urban ecosystem

The urban anthromes or ecosystems are created by urbanization, by transforming wild lands to better meet the needs and desires of humans. Humans govern urban biodiversity directly through habitat loss, habitat fragmentation and the introduction of new species, and indirectly by changing urban climate, soils, hydrology, and biogeochemical cycles (C. E. Adams, 2016; Kowarik, 2011). Beyond physical alterations to the urban environment, socioeconomic activities directly affect biodiversity patterns by setting filters for species selection and dispersal. Both types of mechanisms interact, affect the overall species richness and abundance in urban settings and lead to compositional changes in urban biota (Kowarik, 2011). Since cities are concentrated centers of production, consumption, and waste disposal, urbanization is also a driver of climate change and pollution, altering ecosystem properties even at great distances from urban areas (Grimm et al., 2008; Zhu et al., 2017).

The urban ecosystem is mainly defined by two characteristics: (1) dense concentrations of people, buildings, impermeable surfaces, introduced vegetation which requires much caretaking, and some wildlife species (McCleery et al., 2014); and (2) independence from local natural resources, as the resources imported to persist (food, water and energy) are exported to other landscapes turned into sewage and pollution (C. E. Adams, 2016).

2.1.4. Urban habitats

In urbanized areas, lost natural habitats are replaced by four types of altered habitat either green or gray spaces (Figure 2.2, (C. E. Adams, 2016)).

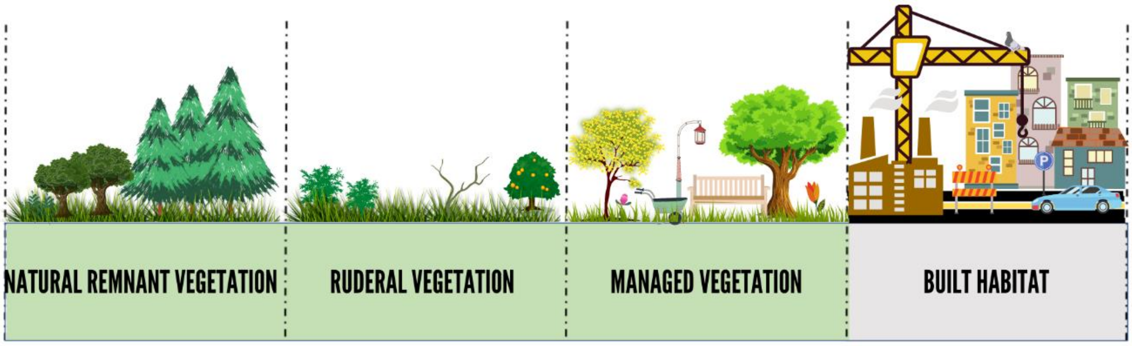


Figure 2.2. Representation of the four types of altered habitat. Designed with Canvas and Freepick.

2.1.4.1. Urban green spaces

Urban green spaces include all-natural, semi-natural, and artificial ecological systems within and around a city (Cilliers *et al.* 2013), comprising a range of habitat types, i.e.: (1) *Natural remnant vegetation*, remaining islands of original vegetation (usually subject to substantial nonnative plant invasion); (2) *Ruderal vegetation*, empty lots, abandoned farmlands, and other green spaces that are cleared but not managed; (3) *Managed vegetation*, residential, commercial, and other regularly maintained green spaces (Aronson et al., 2017). Despite common misconceptions that cities are species-poor, new evidence suggests otherwise, and urban green spaces are vital for supporting urban biodiversity and conservation as well as to provide a range of benefits to humans (Aronson et al., 2014, 2017; Boers et al., 2018; Dearborn & Kark, 2010).

A key challenge for urban green spaces conservation, design, and management is balancing human perceptions, needs, and use with ecological requirements for preserving and enhancing biodiversity (Aronson et al., 2017). Ensuring future urban biodiversity will require effective management of plant and animal populations in urban green spaces, improving their biodiversity potential by enhancing habitat quality and modifying currently common management practices, such as mowing, pruning, and pesticide and herbicide applications (C. E. Adams, 2016; Aronson et al., 2017).

2.1.4.2. Urban gray spaces

Gray spaces are the fourth type of urban habitats, consisting in human-constructed features unique to urbanization and named as (4) *Built habitat*. This is composed by buildings and sealed surfaces, such as roads and parking lots, which cover over 80% of the central urban area.

- Roads

Roads impact on wildlife population dynamics through increasing mortality, loss and change of habitat and biological communities; habitat and population fragmentation and isolation; and disruption of dispersal processes that maintain gene flow within species populations, and therefore, there is a need to develop structures that mitigate the impacts of roads on wildlife populations (C. E. Adams, 2016; Riley et al., 2014).

2.1.5. Wildlife in the urban ecosystem

2.1.5.1. Synurbization

Synurbization can be defined as the response of wildlife to global expansion of urbanization, and is a particular case of synanthropization, the adaptation of animal populations to human-created (anthropogenic) conditions (Luniak, 2004). Urban areas can serve as suitable habitat for wildlife, particularly for those species capable of using highly fragmented habitats. In recent decades, however, urban/suburban landscapes have been infiltrated by other species considered intolerant to human activity until recently. Although wildlife presence in urban settings is perceived as an aesthetic value by part of the human population, the negative consequences of wildlife successfully residing and reproducing in proximity to high human population densities can be substantial (Ditchkoff et al., 2006).

The most characteristic adjustments of synurbic populations are due to the favorable food and climatic conditions of the urban environment, which allow a sedentary life. Consequently, urban wildlife has smaller individual territories and higher population density, prolonged circadian activity and longer longevity. As movement and activity in urban environments can be a high-risk activity, urban conditions also induce changes in the behavior, such as tolerance and tameness towards people, increased intra-specific aggressions, changes in the timing and duration of breeding and altered foraging patterns and diet (Lowry et al., 2013; Luniak, 2004; McIntyre, 2014; Tucker et al., 2020).

2.1.6. Urban ecosystem advantages and threats

Gray spaces can be either favorable or detrimental for wildlife, since they can provide food and shelter but also have measurable impacts on the population dynamics, survivability, and natural history (Study 1, (C. E. Adams, 2016; Rodewald & Gehrt, 2014)).

Urbanization is considered a major threat to biodiversity conservation, as it induces profound landscape transformations (Kowarik, 2011) by an array of anthropogenic factors, including habitat loss and species introductions (Aronson et al., 2014). Urban development removes and fragments habitats, thereby threatening long-term conservation of wildlife species less able to persist in smaller, more isolated habitat patches (McCleery et al., 2014; McIntyre, 2014). However, certain wildlife species are naturally well suited to the altered environment, some are able to adapt to these changes, and others decrease in number or disappear through a combination of mortality and emigration (C. E. Adams, 2016).

A common misconception concerning urban/suburban wildlife is that they are subjected to less stress than their rural counterparts, as food is plentiful and predators are fewer. However, urban individuals are exposed to other stressors substantially constraining the biology and forcing animals to modify their behavior to avoid or mitigate the stress (Ditchkoff et al., 2006). Environmental contaminants produced by anthropogenic activities can have serious, though often cryptic, impacts on the health of wildlife populations, including pesticides (insecticides, herbicides, rodenticides, avicides), industrial byproducts, pharmaceuticals, and fertilizers (C. E. Adams, 2016).

- Anthropogenic food resources

Human provisioning of wildlife with food is geographically widespread, occurs at local and landscape scales and can be intentional or accidental (Becker et al., 2015). Landfills and household waste provide a food source for wildlife, resulting in human–wildlife conflicts (C. E. Adams, 2016; Becker et al., 2018). Urbanization, agriculture and supplemental feeding can supply wildlife with abundant and predictable food (Becker et al., 2018; Ewen et al., n.d.; McKinney, 2006; Newsome & Rodger, 2008). As a result, urban wildlife has adapted foraging behavior to capitalize on these resources(Becker et al., 2018; Sih et al., 2011) , leading to subsidized populations that are often larger, more aggregated and better fed than their naturally foraging counterparts (Becker et al., 2015, 2018; Luniak, 2004; Tucker et al., 2020).

2.1.6.1. Human-wildlife interactions and conflicts

Although rural, suburban, and urban residents generally enjoy wildlife, negative experiences associated with overabundant urban wildlife populations are increasing public concerns (Conejero et al., 2019; Conover, 2002). The close contact between wildlife and humans in urban environments has raised human-wildlife interactions (HWIs), defined as the spatial and temporal concurrence of human and wildlife activities (Leong, 2010; Lischka et al., 2018; Peterson et al., 2010). Human-wildlife conflicts are the results of HWIs when the action of either humans or wildlife affects the other (Conover, 2002; Rakshya, 2016). Out of the urban environment, wildlife damages are usually related to crop depredation, livestock depredation, and property loss, but can also threaten the health of domestic animals and humans by transmitting zoonotic diseases (Hassell et al., 2017; Lloyd-smith et al., 2009; Meng et al., 2009), and even be related to human casualty (Rakshya, 2016). The close contact between urban wildlife and humans enhances some of these risks and hazards, such as zoonotic diseases transmission (Leong, 2010; Lischka et al., 2018; Peterson et al., 2010). Urbanized large mammals also pose risks such as human injury and traffic accidents (Ikeda et al., 2019). Therefore, human wildlife conflicts occur within the SES (Figure 2.2) (Lischka et al., 2018; Rakshya, 2016), and the human dimensions of wildlife conflicts are increasingly being acknowledged as critical (Lischka et al., 2018; Rakshya, 2016; Whittaker et al., 2006).

- Health risk of transmission of zoonotic diseases

As urbanization continues expanding, the risk of outbreaks of emerging diseases resulting from HWIs will continue increasing. The seriousness of SARS-CoV-2 underscores the need of the promotion and further implementation of the One Health Approach (Rabozzi et al., 2012; Zinsstag et al., 2005), the interdisciplinary cooperation among animal, public and environmental health. A growing number of studies indicate that anthropogenic resources can alter host–pathogen interactions, leading to either increased or decreased infection risk for wildlife and humans depending on the nature of provisioning and the particular host–pathogen interaction (Becker et al., 2015). The urban-adapted species sharing habitat and/or interacting with people can serve as hosts, vectors, and reservoirs for zoonotic diseases that pose health threats to humans. Furthermore, the proximity of humans and wildlife in urban areas leads to increased HWIs as compared to other settings, so wildlife have more impact on human health, quality of life, education, and esthetics in urban areas than in any other habitat/environment (McCleery et al., 2014). The cross-species transmission of pathogens among wildlife, humans and domestic animals (Becker et al., 2018; Hassell et al., 2017), could be facilitated by novel assemblages of species formed around anthropogenic resources [14,15, in (Becker et al 2018)], increasing contact rates and facilitating pathogen transmission both within urban wildlife species and among them and domestic animals and humans (Becker et al., 2015, 2018; Hassell et al., 2017; Lloyd-smith et al., 2009; Meng et al., 2009)

Urbanization is likely to have a profound effect on public health as rural pathogens adapt to urban conditions, and other pathogens emerge (or re-emerge) in urban areas (Blancou et al., 2005; Hassell et al., 2017; Rabozzi et al., 2012). Prevention is based on knowledge, but predicting zoonotic diseases outcomes is extremely difficult and poorly understood due to the constantly evolving nature of the multiple factors involved (Meslin, 2008; Rabozzi et al., 2012). To design surveillance systems and enhanced diagnostics of emerging pathogens under new approaches (Burroughs et al., 2002; Rabozzi et al., 2012), improving knowledge about pathogens, vectors and reservoirs, and the complexity of the ecosystem, including temporal and spatial relationships , by examining current zoonotic diseases, is a priority (Burroughs et al., 2002).

Under the scope of the One Health Approach, the risk of human spillover is determined by prevalence of infection in the host population, the rate of contact between humans and infected individuals, and the probability that infection occurs upon contact (Hassell et al., 2017; Lloyd-smith et al., 2009)

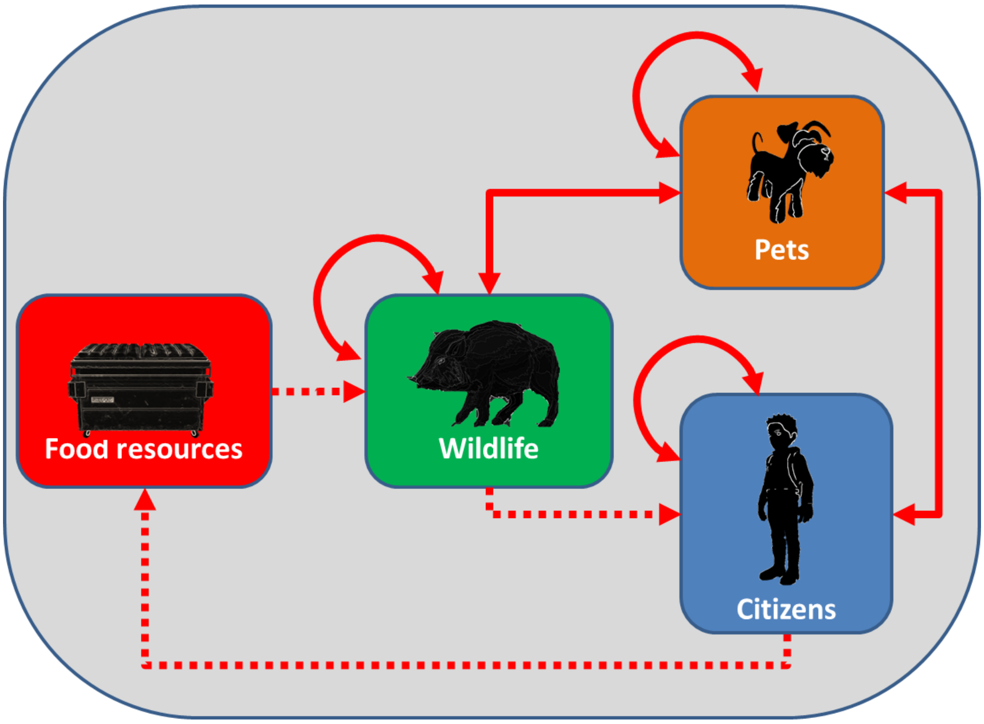


Figure 2.3. Epidemiological processes in urban areas, including the interaction among food resources, wildlife, pets, and citizens. Solid lines represent bidirectional transmission of pathogens. Dashed lines represent unidirectional transmission of pathogens.

2.1.7. Biodiversity management in the urban ecosystems

Studying wildlife dynamics and adaption in urban contexts can provide insights into fundamental evolutionary biology questions, and may inform species and ecosystem conservation and management efforts. If species can adapt to the urban environment, there is a possibility for mitigation of species loss and reclamation of services impaired by diminished biodiversity and ecosystem functions. Researching which aspects of urbanization species are able or unable to adapt to, as well as the timescales needed for adaptation, could provide valuable information for urban planners to facilitate species adaptations (Donihue & Lambert, 2015).

To assess the contribution of cities to biodiversity conservation, the key question is instead whether wildlife, particularly rare and endangered species, do not only occur on urban land but can also establish self-sustaining populations (Kowarik, 2011). The novel urban ecosystems, with the presence of nonnative species, represent profound human-induced changes in natural systems with value as inevitable parts of contemporary landscapes, and therefore, efforts should be aimed to stimulate conservation or restoration approaches (Hobbs et al., 2006; Kowarik, 2018). There is a general need to combine well-established strategies aiming to preserve (semi-)natural remnants and enhance native species in urban regions, those strategies should include approaches that acknowledge the contribution of novel urban ecosystems and associated species assemblages (Kowarik, 2011).

The current goal of wildlife management is to control animal movement and reduce population size in order to avoid human-wildlife conflicts, and changing the recognition and attitude of public towards wildlife (C. E. Adams, 2016; Kansky et al., 2016). However, under the new paradigm of urban ecosystems, where HWIs take place in SES, the goal of wildlife management should aim to identify suitable interventions to increase biodiversity and public knowledge, while using safe, humane, and socially acceptable means (McCleery et al., 2014) to reduce human-wildlife conflicts and mitigate the risk of disease emergence.

2.2. Models

A model is an abstract representation of a reference system, defined to answer questions about this system. This representation is a simplification of the reference system that omits elements considered as irrelevant with respect to these questions (Amouroux, 2011). In the last decades several techniques have been developed, mainly quantitative models, focused on conservation efforts such as Population Viability Analyses (PVAs) and perturbation analyses.

2.2.1. Population Viability Analysis (PVA)

PVAs are model-based quantitative risk assessments that, relying on ecological models, identify viability requirements and threats of a species population, also evaluating the likelihood of persistence, either for a given time under current conditions or after proposed management. PVA-based methods were developed and oriented towards the management of rare and threatened species with the objectives of minimizing the risk of extinction and promoting conditions in which species retain their potential for evolutionary change, without intensive management (Akçakaya & Sjögren-Gulve, 2000; Andersen, 2008). During the recent years, PVAs have also been used in the management of invasive and pest species, as the difference between using PVA to take managing decisions involving invasive or pest species instead of endangered species is that population size reduction is a desirable outcome (Andersen, 2005, 2008)

PVAs commonly incorporate perturbation (i.e., sensitivity and elasticity)analyses (Andersen, 2005). Sensitivity analyses estimate the impact of absolute changes in vital rates on population growth rate λ (λ=e^r, where r is the per capita rate of population increase). By scaling the sensitivities, elasticity analyses estimate the effect of a proportional change in the vital rates on λ in density-independent and time-invariant models. Perturbation analyses have their limitations in considering the impact of each vital rate on fitness as independent, but variation in one vital rate is probably correlated with others (Benton & Grant, 1999).

PVAs can also be used for analyzing monitoring data as a decision-support tool and identifying key life cycle stages and/or demographic processes as targets, focusing on management interventions for established invasive species (Andersen, 2005). The approach is to rely on demographic sensitivity analyses to obtain the desired comparisons (Andersen, 2008). PVAs are also useful to analyze and minimize the financial costs of conservation and control plans, by determining the most cost-efficient management strategies (Duca et al., 2009) and the effect of different management strategies prior to undertaking them. This allows using the available financial resources in the most efficient way and reducing the actions undertaken by estimating their usefulness previously. PVAs have also limitations, such as being usually focused in a single species, needing more data than other methods and producing wide confidence limits of the estimates of extinction time leading to meaningless results, except if used to compare the relative values of different management strategies (Akçakaya & Sjögren-Gulve, 2000; Benton & Grant, 1999).

2.2.2. Agent-based models (ABM)

The limitations of PVAs can be addressed through agent-based models (ABM), also referred to as individual-based models. Agents can be representations of any type of autonomous entity, either animate, such as animals or humans moving freely around an environment, or inanimate, such as plants, with a fixed location but variable state. A collection of multiple, interacting agents, situated within a model or simulation environment is termed an agent-based model. Agent features include autonomy (i.e. governed without the influence of centralized control), heterogeneity (i.e. an animal agent can have attributes such as age, sex, reproductive state, etc.) and active (e.g. pro-active/goal-directed, reactive/perceptive, bounded rationality, interactive/communicative, mobility and adaptation/learning) (Amouroux, 2011). Each agent has a set of virtually limitless attributes, so they can address complex questions about how populations and communities respond to environmental conditions through the effects of those conditions on individuals and the interactions among them (McLane et al., 2011; Zhang & DeAngelis, 2020). ABMs develop in two spatial scales, namely the scale of spatial resolution (spatial area needed in the model), and the scale of spatial extent (size of the area to which the model is being applied) (Zhang & DeAngelis, 2020).

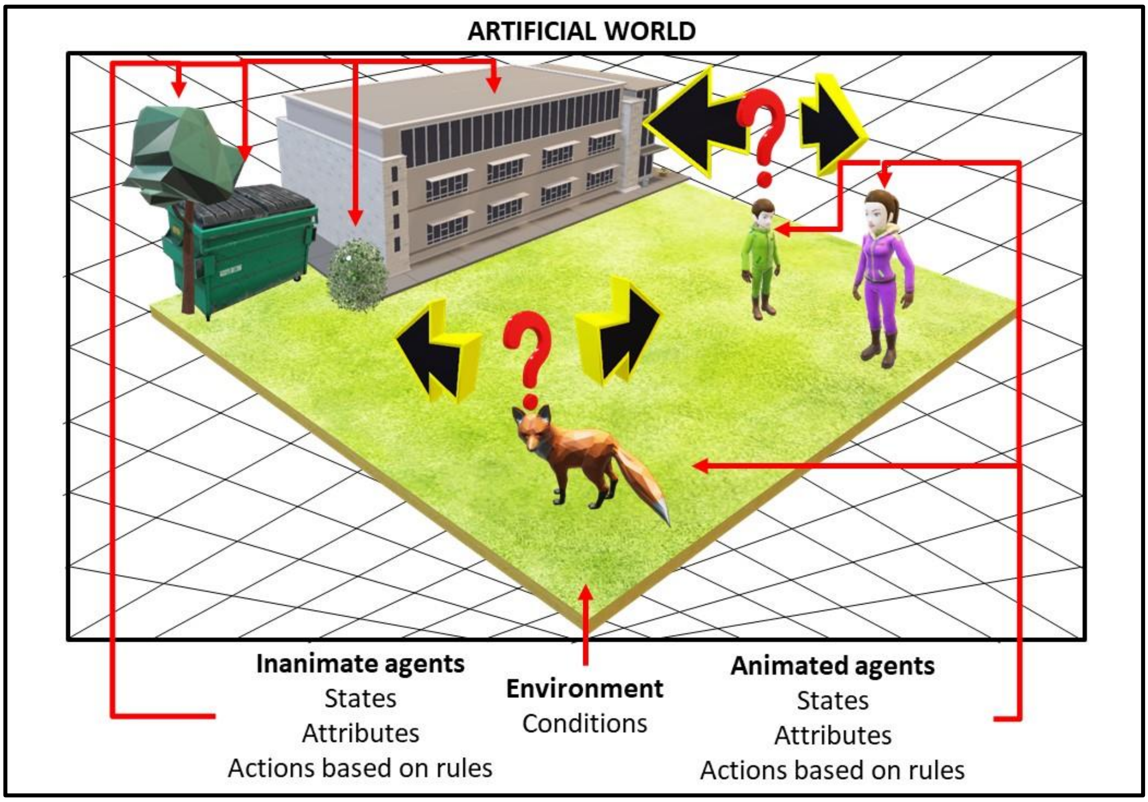


Figure 2.4. Conceptualization of agent-based models.

ABMs differ from other models, such as differential equation (DE) and matrix (MM) models, where a top-down description is determined through population level values (birth rates and mortality at the population level). Conversely, ABMs are bottom-up models where population consequences emerge from the interactions of autonomous individuals among them and with the environment (Amouroux, 2011; Zhang & DeAngelis, 2020). ABMs can be further combined with geographic information system (GIS) capabilities to predict population or community dynamics, by modeling spatially explicit simulations with the actions and relationships among individuals, populations and communities of agents, and their environment (Grimm, 1999; Salinas et al., 2015). The interactions between agents and their environment are the differential trait of agent-based modeling from other systemic modeling approaches (McLane et al., 2011). Besides moving within the environment, agents are aware of it and can respond to changes in their environment, and they can also learn and adapt their state and behavior in response to stimuli from other agents or the environment (McLane et al., 2011).

The whole modeling process involves verification, calibration and validation. Verification checks that the implemented model behaves as expected matching its design. Calibration fine-tunes the model to a particular context by establishing unique values that dimension the model to its data. Finally, validation involves that the model adequately represents the modeled system, making sure that an implemented model matches reality and is related to the extent by the goodness-of-fit of the model to the data (Heppenstall et al., 2012; Xiang et al., 2005)

2.2.3. Applications

ABMs are a versatile tool, well-established and accepted as a suitable methodology for wildlife ecology (Grimm, 1999; McLane et al., 2011). The spatial, temporal, and demographic resolution of ABM, offers managers a decision-making basis to use available empirical data and create resilient management policies by considering multiple possible scenarios, both socio-economic and ecological, with the specific conditions of the simulated system (McLane et al., 2011; Salinas et al., 2015).

2.2.3.1. Wildlife management

Models can be used to identify the vulnerable life stages of pest species and their relative responses to perturbations (Heppel et al., 2000), allowing the establishment of control methods with the proper focus for management effort (Benton & Grant, 1999). The recent proliferation of ABMs in ecological applications, such as addressing HMIs and their management and animal movement and behavior (McLane et al., 2011), is the result of the need in ecology and management for the inclusion of individuality of wildlife species as adaptive, responsive entities (McLane et al., 2011). Models allow defining the most profitable management strategies, and the combination of these, and evaluating the effect of different management strategies before undertaking them.

2.2.3.2. Theorical virtual epidemiology

Understanding how wildlife–livestock–human interfaces and anthropogenic resources alter wildlife infection, cross-species transmission and emergence of pathogens into new host populations, and consequences for spillover risks, is necessary to identify suitable interventions to mitigate the risk of disease emergence, and requires integrating diverse expertise and approaches across multiple levels of biological organization (Becker et al., 2018; Hassell et al., 2017). To increase understanding of the factors and mechanisms influencing the propagation of pathogens, field or *in-vitro* studies results are not completely satisfactory. In this context, theoretical (virtual) epidemiology considers simulated models of reality to test hypotheses concerning factors such as the environment, the social structure and animal behavior (Amouroux et al., 2008).

The most important requirements for virtual epidemiology scenarios to address epidemiological challenges are (1) an extensive representation of the environment and its own dynamics; (2) a framework for both population and individuals; (3) population and/or individual interactions as well as with the environment; (4) data expressed using heterogeneous formalisms able to be reused in the modeling of the system; (5) a simulation platform for virtual scenarios to be run (Amouroux et al., 2008).

2.3. Wild boar

The Eurasian wild boar (*Sus scrofa*) is an artiodactyl of the family *Suidae* with one of the widest geographic distributions of all terrestrial mammals. Originally distributed in Eurasia and northern Africa, after widespread introductions this omnivore species now occurs in all continents except Antarctica, and on many oceanic islands.

Wild boar has spread worldwide in the last decades, mainly due to changes in land use and human population decrease in rural areas, with the consequent decline in traditional activities such as agriculture and forestry (Acevedo et al., 2014; Bosch et al., 2012; Massei et al., 2015) These conditions produced an increase in the total amount of food available and the number of shelter areas, mostly scrub and wooded areas, for wild boar (Bosch et al., 2012). As a generalist species, wild boar is capable of successfully colonizing and exploiting a wide range of habitats (Acevedo et al., 2006), including the interface between urban areas and either forest or agricultural landscapes, and even highly artificial urban green areas (Cahill et al., 2012a; Licoppe et al., 2013).

The population dynamics of wild boar are characterized by a predominance of young animals, with high mortality during the first year of life and high reproductive rates (Herrero et al., 2008). This features allow wild boar populations to response intensely to food, population density and weather conditions, producing sudden increases in numbers followed by high levels of mortality (Massei & Genov, 1997; Servanty et al., 2009). In arid and semi-arid environments like the Mediterranean area, constrains for wild boar populations occurs during summer, when even rooting activity is not possible due to the dry soil (Massei & Genov, 1997)**.** Environmental factors such as food shortage and droughts could affect both survival and reproduction (Massei & Genov, 1997; Servanty et al., 2009).

Food availability has the greater effect on wild boar demography. Enough food availability boosts reproduction, increasing ovulation rate, mean number of fetuses per female, litter size and the percentage of pregnant females, being significant in years of full mast production (Rosell, 1998).Food surplus also increases juvenile survival and lowers the age of first reproduction (Geisser & Reyer, 2005).The proportion of reproducing females can reach up to 90% in good mast years compared to only 20–30% in poor mast years. In dry years, only the females that have completed their corporal development breed and litter size is smaller, accompanied by a higher mortality (Fernández-Llario & Mateos-Quesada, 2005).

2.3.1. Survival

The average lifespan of wild boar under natural conditions is 13 years, but in the Iberian Peninsula rarely reaches more than 11 years, and 5-6 years in Cataluña (Rosell, 1998). According to age-specific variation in demographic parameters three age classes for each sex are defined (Focardi et al., 2008; Servanty et al., 2009; Toïgo et al., 2008): juveniles (0–1 years), yearlings (1–2 years) and adults (> 2 years). The population in mainly composed by wild boars younger than two years (juveniles and yearlings), accounting for 62-79% of the whole population, of which 47% are juveniles (wild boars younger than one year) (Rosell, 1998; Rosell et al., 2001).

The dynamics of most European wild boar populations are strongly influenced by harvest. In a lightly hunted population harvest mortality (11 %) is lower than natural mortality (32%) (Focardi et al., 2008). In such conditions, survival among age classes was constant for females while differed for males, differing between sexes only for yearlings. The survival of juvenile males was correlated with variations in environmental factors and body mass. Conversely, high hunting pressure rose the chance of being harvested annually to40%, achieving 70% for adult males. In such intense hunting conditions, female natural mortality varied substantially whereas male did not, which can be caused by the high energetic investment of wild boar females in reproduction (Toïgo et al., 2008).

2.3.2. Reproduction

Wild boar is the ungulate with the highest fecundity under good conditions (Fernández-Llario and Mateos-Quesada 1998).The mean number of fetuses is four, with range of one to six, and fetal sex ratio does not differ significantly from 1:1 ((Rosell, 1998). Females reach sexual maturity at a minimum weight of 30 kg and minimum age of 6-8 months. During the mating period only the males older than two years are big enough to fight for the females and, thus, participate in the breeding pool (Rosell, 1998)

The size of the litter and the percentage of pregnant females vary more with weight than with age (Boitani et al., 1985). In Mediterranean environments, there is a long birthing period with a peak in April (Boitani et al., 1995; Fonseca et al., 2004). The births occurred after the reproductive peak could be related to a delay in reaching breeding condition by younger females, as well as by part of adult females giving birth three times over two years (Santos et al., 2006). Furthermore, in favorable habitats where nutritious food is available for extended periods and pregnant females have been harvested, the first reproductive period tends to be long and a second reproductive period in August/September might occur (Boitani et al., 1985).

2.3.3. Movement

Animals are able to locate themselves and navigate using two sources of information, allothetic and idiothetic cues, which define the navigation process and the strategy used. In the Piloting strategy, animals use the allothetic navigation, depending on the relationship of external cues such as visual, auditory, and olfactory with spatial maps. Conversely, in the Dead reckoning strategy, animals use idiothetic navigation, relying on cues generated by self-movement, such as proprioceptive cues and path integration (Whishaw et al., 2001).

2.3.4. Role of wild boar as a multi-host species

Wild boar plays a major epidemiological role as host for zoonotic and non-zoonotic pathogens shared with livestock, companion animals and humans(Fernández et al., 2006; Hassell et al., 2017; Lloyd-smith et al., 2009; Meng et al., 2009; Ruiz-Fons, 2017). Wild boar is therefore potential source for emerging human diseases (Meng et al., 2009; Ruiz-Fons, 2017), participating in the maintenance of multi-host pathogens (Haydon et al., 2002; Viana et al., 2014). The relevance of wild boar in the epidemiology of shared diseases from a One Health Approach (Gortázar et al., 2007) is enhanced in the urban context (see section 2.3.6).

Hepatitis E virus (HEV) is a single-stranded, positive-sense RNA virus, classified in the family *Hepeviridae*. The strains infecting mammals are classified in the genus *Orthohepevirus,* with five genotypes infecting humans (Wang et al. 2019). HEV3 and HEV4 genotypes are zoonotic viruses shared with pigs worldwide, thus, wild boar may constitute true reservoir host for HEV (Ruiz-Fons, 2017)
. The BMA wild boar population has a 20% prevalence (20%) of HEV infections (HEV3 genotype, subtypes 3f and 3c/i), indicating that zoonotic transmission from wild boar may be more common than previously anticipated (Wang et al. 2019).

Campylobacter spp. And *Escherichia* spp. (Castillo-Contreras, 2019), are also both a public health concern. Campylobacteriosis is considered the most common bacterial cause of human gastroenteritis worldwide (WHO, 2019). WB constitutes a reservoir of *Campylobacter* species, including antimicrobial resistant and multi-resistant strains (Carbonero et al., 2014; Castillo-Contreras, 2019). *Campylobacter* can be transmitted to humans from animals or animal products, most often from feces (WHO 2020). Most (60.8%) WB in the BMA carried *Campylobacter* spp. Thirty-five per cent of the isolates had high virulence genes and all the *Campylobacter* isolates tested were resistant to at least one antimicrobial, 68.2% of them multi-resistant (Castillo-Contreras, 2019).

AFSV, an OIE (World Organization for Animal Health) List A virus, is a DNA virus in the family *Asfarviridae* (Meng et al., 2009). ASFV is highly contagious, affecting domestic pigs and WB with fever, hemorrhages and resulting in up to 100% morbidity and mortality in previously unexposed WB with no treatment or vaccine (Costard et al., 2013; EFSA, 2014). It is transmitted through direct contact, ingestion of contaminated feed stuffs and ticks (EFSA, 2014). The current European wild boar density appears to facilitate the onset of ASFV and the role of the species as reservoir for this virus (More et al., 2018).

The recent emergence and spread of ASFV in several Eastern and Central European countries (Arias et al 2013) are linked to the movement of both wild boar and anthropogenic resources (De la Torre et al., 2015; Guinat et al., 2016). The pork industry is a major economic sector in Catalonia (Spanish administrative region where the BMA is located), with 5,930 pig farms and 9,414,802 pigs in 2019 (Departament d’Agricultura, Ramaderia, Pesca I Alimentació, Generalitat de Catalunya, 2019a)., accounting for

2.646 million Euros in exports in 2019 (PRODECA and Departament d'Agricultura, Ramaderia, Pesca I Alimentació, Generalitat de Catalunya, 2020).

ASFV is a major concern for national and regional governments because the devastating economic impact for the pork industry associated to high morbidity and mortality and trade restrictions (Castillo, 2019; Gavier-Widén et al., 2015; Sánchez-Cordón et al., 2018). Due to the human origin of ASFV outbreaks, particularly of those distant from the distribution area of the disease, the growing human-wild boar interface at the BMA is a potential origin for an ASFV outbreak in the region.

2.3.5. Urban wild boar

As a result of the combination of increasing WB populations and synurbization processes (Luniak, 2004), wild boar is colonizing urban areas (Cahill et al., 2012ª; Castillo-Contreras et al., 2018; Podgórski et al., 2013; Stillfried et al., 2016; Toger et al., 2018). In the particular case of wild boar, the synurbization process is originated by a higher tolerance to human disturbance (Stillfried, Gras, Börner, et al., 2017), lack of natural predators and the availability of using anthropogenic resources (Castillo-Contreras et al., 2018; Llimona et al., 2007). The conditions in the urban environment provide to the urban populations an advantage over natural populations. These differences are especially relevant during the scarcity periods through the year, summer in Mediterranean areas, changing the population dynamics by reducing mortality and increasing fertility, therefore boosting abundance as described in other synurbic species (Luniak, 2004).

2.3.6. Human-wild boar conflicts

The increase in wild boar population and proximity to urban areas have raised both impact on the ecosystem and conflicts with humans. Wild boar causes damage to crop fields in cultivated areas, to plant diversity, vegetation composition and regeneration patterns (Geisser & Reyer, 2005; Massei & Genov, 2004), predates on a number of species (Massei et al., 2011) and provokes traffic accidents (Cahill et al., 2012a; Licoppe et al., 2013; Rosell et al., 2001; Tenés et al., 2007).The colonization of urban areas and habituation to humans also causes damage to urban green areas, attacks on people and pets, and supposes a health risk (Cahill and Llimona 2004, Seán Cahill et al. 2012*a*, Licoppe et al. 2013; Wang et al. 2019).

These conflicts have generated consequences in the SES of the human-wildlife interactions (Lischka et al., 2018). In the ecological system, it has produced changes in population dynamics, animal behavior and ecosystem imbalance due to overpopulation (Lischka et al., 2018; Tucker et al., 2020). In the social system, it has resulted in economic consequences such as the increase in public expenses related to restoring street furniture and green areas, capturing problematic individuals and police interventions, as well as private expenses related to green areas, plantations and facility restoration.

2.3.6.1. Epidemiological risk

Wild boar presence in urban areas also has public health consequences, such as intraspecific disease transmission and disease sharing with humans and pets. The epidemiological role of wild boar becomes more relevant in urban areas, where the anthropogenic resources foraged by synurbic WB are amplifiers of pathogen invasion by increasing host aggregation and tolerance (Becker et al., 2015). Human activities may be the source, influencing the carriage and potential spread of antimicrobial resistant bacteria on wild boar (Castillo-Contreras, 2019; Navarro-Gonzalez et al., 2018; Swift et al., 2019; Vittecoq et al., 2016). Under these circumstances, changes in host contact rates and immunity can produce strong non-linear responses in pathogen invasion and prevalence (Becker et al., 2015). Moreover, the increased aggregation produced by anthropogenic resources in urban areas increases the contact rates of synurbic wild boars and humans (Becker et al., 2015, 2018; Castillo-Contreras et al., 2018; Toger et al., 2018), the risk of exposure to pathogens and therefore, the concern about the role of wild boar as a potential source for emerging human diseases (Blancou et al., 2005; Hassell et al., 2017; Meng et al., 2009; Ruiz-Fons, 2017).

2.3.6.2. Management challenges

There is a generalized need for wild boar management plans (Geisser & Reyer, 2005), due to the challenging increase in wild boar numbers in Europe, the consequently increase in ecological and economic consequences, the absence of a realistic solution and the rarely considered extensive economic costs of wildlife management by traditional models (Baxter et al., 2006).

2.3.7. Wild boar in Collserola Natural Park

Along the worldwide trend, wild boar population has increased in the province of Barcelona (Northeastern Spain) over the last two decades (Cahill & Llimona, 2004; Rosell, 1998). Collserola Natural Park (CNP) is a green island of 80 km^2acknowledged as a Natura 2000 site, surrounded by urban areas inside the Barcelona metropolitan area (BMA), with 3.2 million people, occupying 636 km^2 (population density of 5000 people per km^2) (BMA 2020). Wild boar population in the CNP has not only increased in number, but has also become habituated to human presence over the last ten years, due to both direct and indirect anthropogenic feeding (Cahill et al., 2012a; Castillo-Contreras et al., 2018). This occurs particularly in the peri–urban area of Barcelona, as well as other nearby cities surrounding the CNP, facilitated by the proximity of densely vegetated areas close to the city limits (Cahill et al., 2012a, 2012b; Llimona et al., 2007). Previous epidemiological studies on the BMA wild boar population have detected zoonotic hepatitis E virus (Wang et al., 2019), *Streptococcus suis* (Fernández-Aguilar et al., 2018), tick-borne pathogens such as *Rickettsia* spp. (Castillo-Contreras, 2019), and antibiotic resistant bacteria such as *Escherichia coli*, *Enterococcus faecalis*, and *Enterococcus faecium* (Castillo-Contreras, 2019; Navarro-Gonzalez et al., 2018).

This thesis identifies the most efficient management strategies to reduce the associated consequences of the presence of wild boar in urban areas (Study 1), evaluates the use of spatially-explicit models to understand the synurbization of wild boars in the Metropolitan Area of Barcelona (BMA) (Study 2),and evaluates the potential epidemiological risk of synurbic wild boars to both, the wild boar population and public health in the Metropolitan Area of Barcelona (BMA) (Study 3).

3. HYPOTHESES

The hypotheses of this thesis are:

1. Models, such as sensitivity test, population viability analyses (PVA) and agent-based models (ABM), are useful tools for decision-making in wildlife management and epidemiological risk assessment and surveillance (studies 1, 2 and 3).

2. Population Viability Analysis (PVA) can identify the most efficient management strategies to target wild boar population abundance and consequently likely decrease the associated conflicts (study 1).

3. ABM can capture the social-ecological system of human-wild boar interactions in (peri)urban environments (study 2).

4. The spatial risk of human and wild boar exposure to selected pathogens carried by wild boars in (peri)urban environments can be assess through ABM, allowing the establishment of management measures (study 3).

4. OBJECTIVES

Consequently, the objectives of this thesis are:

1. Identify, by means of sensitivity test, the variables driving the wild boar population dynamics in Collserola Natural Park (CNP) (study 1).

2. Evaluate, by means of population viability analyses (PVA), the effect of management strategies on the wild boar population of the Collserola Natural Park (CNP) (study 1).

3. Develop of a spatially explicit agent-based model (ABM) capturing the social-ecological system of human-wild boar interactions in Barcelona, integrating wild boar infiltration, urban structure on a fine scale, and human activity (study 2).

4. Evaluate and predict, by means of an agent-based model (ABM), the presence of WB in Barcelona and Collserola Natural Park (CNP) (study 2).

5. Evaluate and predict, by means of an agent-based model (ABM), the public health risk of zoonotic hepatitis E virus (HEV) and antimicrobial-resistant *Campylobacter* (AR-CB) posed by wild boars in the urban area of Barcelona and Collserola Natural Park (CNP) (study 3).

6. Evaluate and predict, by means of an agent-based model (ABM), the consequences of a potential outbreak of African swine fever (ASFV) in the wild boar population of Collserola Natural Park (CNP) (study 3).

5. STUDIES

5.1. Study 1

Stochastic assessment of management strategies for a Mediterranean (peri)urban wild boar population

PLoS ONE (2018) 13(8)

DOI 10.1371/journal.pone.0202289

5.1.1. Abstract

Wild boar (WB, *Sus scrofa*) population spread into urban and (peri)urban areas has exacerbated conflicts with humans. There is a need for planned WB management strategies, and Population viability analysis (PVA) combined with perturbation analyses allow the assessment of the management effort of control methods. Our study aims to develop stochastic predictive models of the increasing WB population of the 80 km^2 (peri)urban Mediterranean area of Collserola Natural Park (CNP), located near Barcelona, Spain, as well as assessing specific management measures (including reduced food availability, selective harvest, and reduction in fertility). Population parameters were estimated from previously published census and hunting data provided by the CNP and the local hunting administration. The results revealed that under the current conditions the CNP WB population will continue to increase. The most efficient strategy to reduce WB abundance was a combination of reducing supplementary anthropogenic food resources and selective removal of juvenile (<1 year) and yearling (1-2 years) WB. These strategies will probably be also the most efficient ones in other oversupplemented increasing WB populations in similar situations, although specific studies will be needed to fine-tune the best management option for each context. PVA allows the prediction of future population trends and the assessment of the efficacy and efficiency of potential management strategies before implementing management measures.

Key words

Barcelona, damage management strategies, metropolitan areas, stochastic population modelling, *Sus scrofa*, urbanization, vertebrate pest control, WB.

5.1.2. Introduction

Wild boar (WB, *Sus scrofa*) population numbers have increased and their distribution area has spread worldwide in the last decades, mainly due to artificial feeding, a reduction in predators and translocations (Herrero et al., 2008),changes in land use and decrease of human population in rural areas (Acevedo et al., 2014; Bosch et al., 2012; Massei et al., 2015). At least in Europe, climate change is also favoring WB populations through milder winters and increased mast productivity (Vetter et al., 2015). As a generalist species, the WB is capable of successfully colonizing and exploiting a wide range of habitats (Acevedo et al., 2006), including the interface between urban areas, agricultural landscapes and even highly artificial urban green areas (Cahill et al., 2012a; Licoppe et al., 2013).

Increasing WB population in rural areas and in proximity to urban areas has exacerbated conflicts with humans. WB cause damage to crop fields in cultivated areas, to plant diversity, vegetation composition and regeneration patterns (Geisser & Reyer, 2005; Massei et al., 2011), they prey on a number of animal species like ground-nesting birds, such as red-legged partridge (*Alectoris rufa*), pheasants (*Phasianus colchicus*), mammals as the red-backed vole (*Clethrionomys gapperi*) and short-tailed shrew (*Blarina brevicauda*) and even domestic livestock(Massei & Genov, 2004). WB are increasingly involved in vehicle collisions (Cahill et al., 2012a; Licoppe et al., 2013; Rosell et al., 2001; Tenés et al., 2007). The colonization of urban areas and habituation to humans has also increase damage in parks, green areas, attacks on people and pets, and pose human-health risks (Cahill et al., 2012a; Cahill & Llimona, 2004; Licoppe et al., 2013).

Regulated WB hunting has been the primary method of population control. However, WB hunting is declining in some European countries and is currently insufficient to halt WB population growth (Massei et al., 2015). Suggested methods to control the growth of WB populations include the use of toxicants, not approved in Europe but common in other parts of the world such as Australia (Hone, 2012) and fertility control (Massei et al., 2011; Pepin et al., 2017). Other methods are aimed to decrease damage and conflicts like the use of repellents, translocation and fencing (Geisser & Reyer, 2004; Massei et al., 2011). However, none of these methods provides a definitive solution to control population growth because the high reproductive rate of WB compensates for the potential mitigation effects of these measures (Geisser & Reyer, 2004; Servanty et al., 2011).

There is a general need for carefully planned WB management strategies (Geisser & Reyer, 2005). Identifying the vulnerable life stages of pest species and their relative responses to perturbations (Andersen, 2005; Heppel et al., 2000) allows the establishment of control methods within the proper focus for management effort (Benton & Grant, 1999). Population viability analysis (PVA) combined with perturbation analyses (i.e. sensitivity and elasticity) are currently the most commonly used methods for this objective (Andersen, 2005).

Population Viability Analysis (PVA) is a model-based quantitative risk assessment that, relying on ecological models, identifies the viability requirements and threats to a species population, also evaluating the likelihood of persistence, either for a given time under current conditions or expected from proposed management. Although PVAs were originally developed for threatened species to evaluate the risk of extinction allowing to minimize the risks (Akçakaya & Sjögren-Gulve, 2000; Andersen, 2008),they have also been used to evaluate the impact of disease outbreaks (Serrano et al., 2015) and to assess the effects of management measures aimed at reducing population size for invasive and pest species (Andersen, 2005, 2008).

Both PVA and sensitivity analyses can also be used as a decision-support tool to identify key life cycle stages and/or demographic processes as targets for management interventions for established invasive species (Andersen, 2005, 2008). This allows the determination of the most cost-efficient management strategies (Duca et al., 2009) and the effect of different management strategies prior to undertaking them.

The purpose of our study was to develop stochastic predictive models of the WB population of the (peri)urban Mediterranean area located near Barcelona, Spain. We specifically wanted to use sensitivity analyses (Andersen, 2008) to identify the life stages (sex and age) to be targeted with specific management measures (including reduced food availability, selective harvest, and reduction in fertility), in order to achieve the maximum effect for population reduction (Focardi et al., 1996); and, secondly, to evaluate the effectiveness of the aforementioned management strategies on affecting the most vulnerable life stages and thereby controlling population growth. The results will provide managers with measures that can be applied to reduce WB populations and the attractiveness of urban areas for this species in Mediterranean ecosystems.

5.1.3. Methods

Our study area consisted of the 80 km^2 Natura 2000 Collserola Natural Park (CNP) (41°25'52''N, 2°4'45''E), located in Barcelona, in north-eastern Spain, WB are considered abundant in the province of Barcelona (Cahill & Llimona, 2004; Rosell, 1998).The CNP (Figure 5.1) is surrounded by urban areas within the Barcelona metropolitan area (BMA). The BMA is one of the largest European metropolitan areas, with 36 municipalities occupying more than 636 km^2 and populated by 3.2 million people (population density of 5,000 people per km^2) (Àrea Metropolitana de Barcelona, 2015).

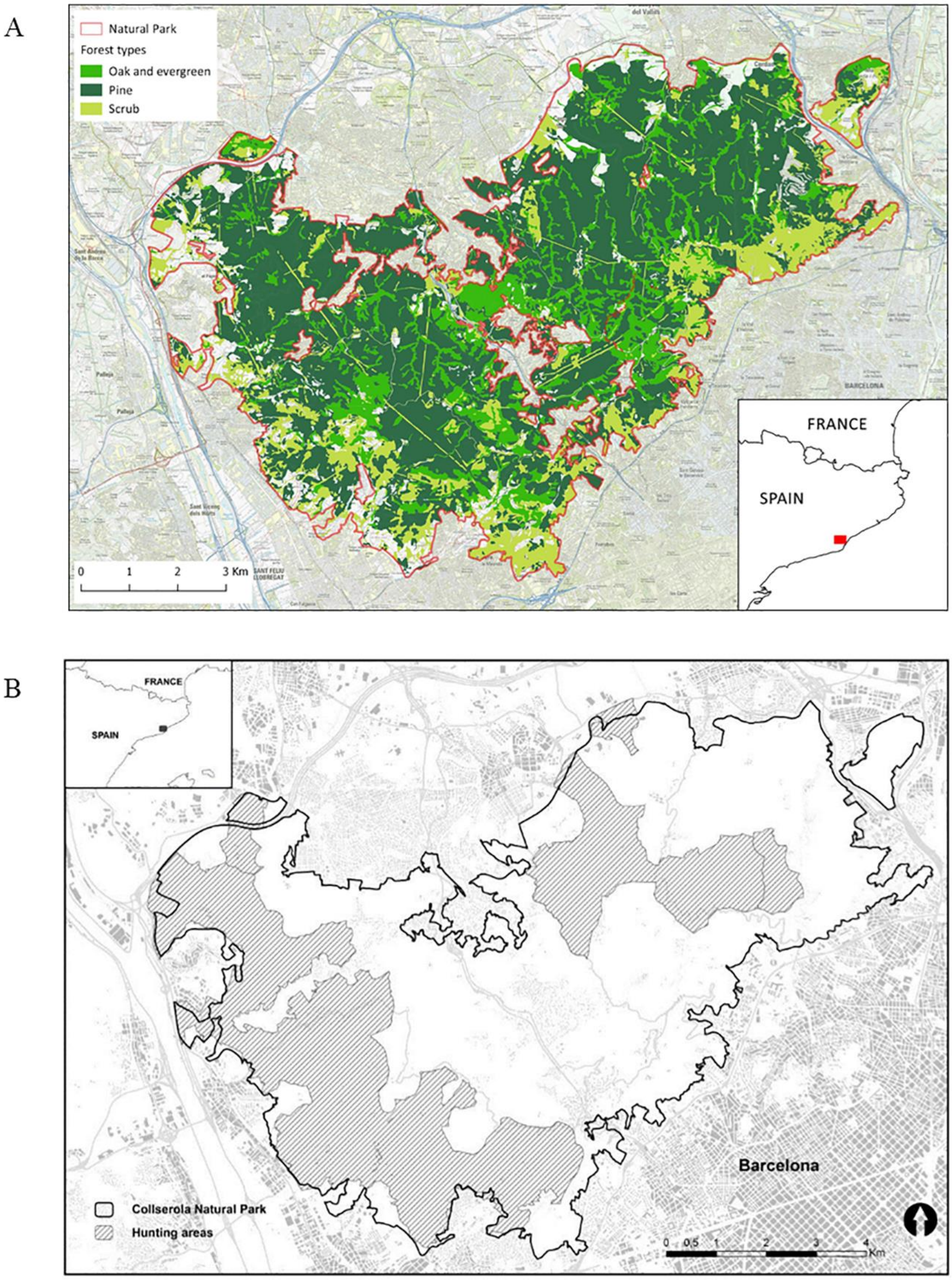


Figure 5.1. Study area. Maps of Collserola Natural Park, Barcelona, NE Spain, showing a) the different habitats and b) Controlled Game Area, currently the only hunting areas in the whole massif.

The CNP is virtually isolated from the nearby natural and agricultural areas by urban development and road and train networks (Figure 5.1A) (Cahill & Llimona, 2004), although some corridors and ecological connectors, such as riparian areas and dry riverbeds, are used by WB, hence allowing some movements out of this area (Castillo-Contreras et al., 2018). The CNP is a Mediterranean hilly area, with an altitude ranging from 60 to 512 meters at the Tibidabo summit. The climate is typically Mediterranean, with warm dry summers and mild wet winters. Annual rainfall is 672 mm and average annual temperatures range from -4ºC (minimum) to 35ºC (maximum).The vegetation of CNP is mainly composed of Mediterranean scrub (24%) and mixed woodland of Aleppo pine (*Pinus halepensis*) (40%) combined with evergreen oak (*Quercus ilex*) (15%) and deciduous oak (*Q. cerrioides*) (0.7%) (Cahill et al., 2012a; Pérez-Haase & Carreras, 2012). The remaining surface is composed by abandoned fields, wastelands and ruderal areas (3.9%), urban areas (3.5%), herbaceous (2.1%) and woody (1.8%) croplands and others (i.e. grasslands, ports, rafts, artificial canals, etc.) (9.0%). Oak acorn production in Mediterranean areas is highly variable, both intra- and inter-annually, mainly due to spring weather conditions during flowering and acorn growth (Fernández-Martínez et al., 2012; Koenig et al., 2015). Inter-annual evergreen oak production variation in Catalonia ranges from 58 to 82% (Herrera et al., 1998), and a full mast year takes place every four years on average (Herrera et al., 1998; Rodríguez-Estévez et al., 2007). The WB is the only wild ungulate and the largest animal in size inhabiting the CNP. Although some minor piglet predation by medium-sized carnivores such as foxes may happen within the park, no natural predators for adult WB thrive inside the park. Therefore, natural predation is likely negligible and has no impact on the WB population dynamics.

The WB population in the CNP has increased and become habituated to human presence, due to anthropogenic resources, including street bins, waste containers, stray cat colonies, urban green areas and direct feeding by people (Figures S5.1A and S5.1B in) (Castillo-Contreras et al., 2018). Anthropogenic feeding is facilitated by the proximity of densely vegetated areas close to the city limits (Cahill et al., 2012a, 2012b; Llimona et al., 2007).

In CNP, hunting is allowed from October through February as a traditional activity with a management plan in the Controlled Game Area of Collserola, which comprises 38% of the CNP surface and the same proportion of habitats described for the CNP (Figure 5.1b). Hunting is carried out via drive hunts with hunters at fix positions and hound packs flushing the boars, in about 17.2% of the park. In an attempt to reduce WB abundance and damage, hunting pressure has progressively increased since 2004 through night waits (single hunter from a fix position, using bait and spotlights but not hide), granted almost year-round even in non-hunting areas after damage claims(Cahill et al., 2012a).

In spite of such hunting pressure, the estimated CNP WB population has experienced a 10-fold increase from 2000 to 2015, reaching an estimated relative abundance of around 1,500 WB (Table 5.1). The estimated percentage of harvested WB with respect to the estimated WB population increased throughout the study period from 10.0% (2000-2003) to 46.5% (2012-2015) (Table 5.1). However, adults were overrepresented (65.6%) in the battue hunting bag as compared to their proportion in Mediterranean populations (25%) (Boitani et al., 1995; Focardi et al., 2008; Herrero et al., 2008; Servanty et al., 2011), whereas yearlings and juveniles accounted only for 34.4% of the total harvest, far less than their proportion (75%) (Herrero et al., 2008). Although the scarce detected poaching has been included in the mortality rate, both the amount of WB poached and the effect of poaching on the CNP WB population are negligible.

Table 5.1. Wild boar harvested and abundances in Collserola Natural Park from 2000 to 2014.

Year	Hunting season	Estimated WB population in CNP (CI 95%)	WBs hunted in drive hunts	WBs hunted in night waits	Registered mortality (% of the estimated population)$^{+}$
2000	2000/2001	165 (0.0-371.4)	19	0	19 (11.5)
2001	2001/2002	357 (167.8-546.2)	35	0	35 (9.8)
2002	2002/2003	191 (15.4-366.6)	18	0	18 (9.4)
2003	2003/2004	280 (98.0-462.0)	27	0	27 (9.6)
2004	2004/2005	579 (400.2-757.8)	61	19	128 (22.1)
2005	2005/2006	-	26	35	129
2006	2006/2007	558 (295.7-820.3)	26	43	136 (24.4)
2007	2007/2008	689 (485.5-892.5)	77	37	173 (25.1)
2008	2008/2009	-	29	44	171
2009	2009/2010	809 (580.1-1,037.9)	50	53	168 (20.8)
2010	2010/2011	821 (608.0-1,034.0)	72	77	222 (27.0)
2011	2011/2012	773 (458.5-1,087.5)	84	108	269 (34.8)
2012	2012/2013	1,050 (786.1-1,313.9)	109	171	462 (44.0)
2013	2013/2014	759 (596.1-921.9)	114	261	486 (64.0)

2014	2014/2015	831 (662.6-999.4)	75	206	326 (39.2)
2015	2015/2016	1,500 (1,296.5-1,703.5)	123	432	650 (43.3)

+ Including all the WB hunted, killed in car accidents, poached and captured and euthanized.

Fertility control of the WB population of the CNP has not been attempted, and repellents are unlikely to be effective in reducing the impact of WB (Massei et al., 2011). Finally, fencing of CNP is incompatible with the human uses of this natural area surrounded by a 3.2 million human population.

All the data have been gathered from hunting records and WB management projects but no WB has been hunted, captured, handled or euthanized for this study.

Data collection

Sex, age and abundance data for the local WB population (Table 5.1 and 3.2) were collected by the authors from WB captured, hunted or found dead from 2000 to 2015. According to age-specific variation in demographic parameters we defined three age classes for each sex (Focardi et al., 2008; Servanty et al., 2009; Toïgo et al., 2008): juveniles (0–1 years), yearlings (1– 2 years) and adults (> 2 years). Specific age class abundances were calculated from the aforementioned data collected by the authors and were used to calculate the specific age class mortality rates (Table 5.2).

Table 5.2. Input data used in the model scenarios of the Collserola Natural Park WB population. Life history and population attributes: A) Reproduction values; B) Mortality and environment values. EV: Environmental variation.

A			
Parameters		**Base value**	**Source**
Breeding system		Polygynous	(Rosell et al., 2001)
Age of first offspring (year)	Females	1	(Rosell, 1998; Rosell et al., 2001)
	Males	2	
Maximum age of reproduction (year)	Female	11	(Rosell et al., 2001)
	Male	11	
Maximum lifespan (years)		11	(Rosell et al., 2001)

Maximum of broods per year			2	(Boitani et al., 1985; Santos et al., 2006)
Maximum of progeny per brood			6	(Rosell et al., 2001)
Sex-ratio at birth			1:1	(Rosell, 1998)
% females breeding (SD due to EV)	0-1 years		15 (10)	(Rosell, 1998; Rosell et al., 2001)
	1-2 years		60 (10)	
	> 2 years		70 (10)	
Distribution of broods per year	0 broods		10	(Boitani et al., 1985; Santos et al., 2006)
	1 brood		85	
	2 broods		5	
Number of offsprings	Mean (SD)		3.5 (2)	(Rosell, 1998)
% males in the breeding pool			25	(Rosell, 1998)
B				
Parameters			**Base value**	**Source**
Mortality rates[+] Mean as % (SD due to EV)	Females	0-1 years	29 (10)	Present study
		1-2 years	35 (10)	
		> 2 years	39 (10)	
	Males	0-1 years	30 (10)	
		1-2 years	43 (10)	
		> 2 years	35 (10)	
Catastrophes				
1) Severe drought				
Frequency			15%	Servei Meteorologic de Catalunya, unpublished data
Severity	Reproduction[a]		0.5	(Fernández-Llario & Carranza, 2000; Fernández-Llario & Mateos-Quesada, 2005; Rosell, 1998)

	Survival[b]	0.5	(Focardi et al., 2008; Geisser & Reyer, 2005; Massei & Genov, 1997)
2) Full mast			
Frequency		22%	(Herrera et al., 1998; Rodríguez-Estévez et al., 2007)
Severity	Reproduction[a]	1.5	(Rosell, 1998)
	Survival[b]	1.5	(Geisser & Reyer, 2005)
Carrying capacity (K)			
K value (SD due to EV)		3000 (150)	Present study

[+]We estimated the age-class survival rates (Sac) from hunting data using the formula (Akçakaya et al., 1999; Lacy et al., 2015): $\boldsymbol{Sac} = \frac{\sum \boldsymbol{Nac+1(tx+1)}}{\sum \boldsymbol{Nac(tx)}}$, where$Nac$ and $Nac+1$ are the abundances of the ageclasses, and tx the census years. *Nac* were calculated from data collected by the authors.

[a] Proportion of WB reproducing.

[b] Proportion of WB surviving.

Population trend was estimated from hunting bags only from the drive hunt data (Table S5.2), a reliable index of WB relative abundance (Boitani et al., 1995). Briefly, the number of WB hunted in every hunting event is divided by the hunted surface. This value is corrected by the mean efficiency of the hunting season (total WB hunted divided by the total WB seen in all the drive hunts of the year) and the result is again divided by the ratio between the number of hunting events in a season and the mean annual number of hunting events. This method was used consistently during the whole study period with minor variations among years (except for 2005 and 2008) in the independent variables: number of drive hunts (18.4 SD 0.97), number of hunting days (9.2 SD 0.48), hunters in each drive hunt (44.1 SD 3.43) and dogs in each drive hunt (46.5 SD 2.96).

We obtained reproductive data (Table 5.2) from literature review on WB biological parameters in neighboring populations in Mediterranean environments (Fonseca et al., 2004; Herrero et al., 2008; Rosell, 1998; Servanty et al., 2011).

To provide a carrying capacity (K value) allowing to perform our PVA with VORTEX (Lacy, 2005), we defined a hypothetical population threshold (HPT) fixed to a number of 3,000 individuals. This value falls just between the 1,000 WB value corresponding to a density of 12.5 WB/km^{2}in the 80 km^2 CNP (Massei et al., 1996; Rosell et al., 2001), and the 6,400 WB corresponding to the maximum WB population density value recorded in fenced, food, water and shelter-supplemented Mediterranean environments (80 WB/km^2, Gonçalves-Blanco, Ingulados Co., personal communication).

To include environmental stochasticity in the model, we considered the plasticity of Mediterranean WB populations, modeling a population characterized by high reproductive rates and high mortality in the first year of life (Herrero et al., 2008), intense responses to food availability and weather conditions, with the proportion of reproducing females varying from 20-30% to 90% depending on food resource availability (Massei et al., 1996; Massei & Genov, 1997; Servanty et al., 2009). Altogether allows the population to increase even under yearly hunting pressures over 50% (Toïgo et al., 2008).

Modeling

The trend of the CNP WB population was modeled from the published and estimated data (Table 5.2) over a time frame of 36 years (2000-2035) through two scenarios: past and future. We carried out simulation models using VORTEX Version 10.0.8 (Lacy, 2005), a free software developed by the Chicago Zoological Society. The software is an individual-based simulation model for PVA that modeled the effect of deterministic and stochastic processes on the dynamics of wildlife populations (Lacy et al., 2015).

We ran 500 iterations for each scenario to allow standard error calculations and we delayed the first year mortality until all annual mortality was done (Lacy et al., 2015), in order to allow the harvest of juveniles. We included the vortex option of “environmental variation concordance of reproduction and survival” as the environmental variation affect reproduction and survival simultaneously (Massei & Genov, 1997; Servanty et al., 2009) but not inbreeding effects, nor genetic management or density dependence effects on reproduction in the model.

Past scenario-We ran a 16-year (2000 to 2015) simulation with an initial population size of 165 WB (the estimated population size in 2000, CNP) to validate the model. We used the HPT value (3,000 individuals) and the parameter values introduced in VORTEX (Table 5.1). The number of WB of each age class harvested each year was modeled through a function (Table S5.1).

Future scenario- A 20-year projection was run to study the future evolution of the population and to test both the impact of the variation in demographic rates and management strategies on the CNP WB population trend. The values for the parameters were taken from the past scenario, initiating the model with a WB population size of 1,500 individuals in 2015 (as estimated by the hunting bag analyses and confirmed by the past scenario model). Harvest was calculated to remain at 30 % of the population, maintaining the same harvest proportion of each age-class as in the past scenario, and it was modeled by a function (Table S5.1). We evaluated three HPT values (3,000, 4,200 and 6,400), corresponding to three different situations depending on the availability of anthropogenic resources under the same management.

Sensitivity and elasticity analyses

Sensitivity and elasticity analyses estimate respectively the impact of absolute and proportional changes in biological parameters on population growth rate (Benton & Grant, 1999). We tested the sensitivity and elasticity of the CNP WB population parameters on WB population trend in the CNP for 25 years in the future scenario, using the Sensitivity test (ST) implemented in VORTEX 10. We measured the sensitivity or impact as the total variation in the projected population sizes between the minimum and maximum value of the variable, and the elasticity or effect as the average population variation corresponding to each 10% parameter variation. The demographic variables were modified as follows to estimate the effect of three main different management strategies: 1) decreasing CNP HPT for WB (minimum value 500, maximum value 6,500, increment by 500) corresponding to different levels of anthropogenic food availability (Bieber & Ruf, 2005; Geisser & Reyer, 2004, 2005; Massei et al., 2011); 2) reducing the percentage of breeding males and females (minimum value 0, maximum value 100, increment by 10) in each age-class through fertility control corresponding to variable fertility control effort (Massei et al., 2011; Servanty et al., 2009); and 3) increasing mortality (minimum value 0, maximum value 100, increment by 10) in sex and age-classes and a combination of them corresponding to variable and selective harvest pressure (Bieber & Ruf, 2005; Geisser & Reyer, 2004; Herrero et al., 2008; Servanty et al., 2011; Toïgo et al., 2008). We also ran a factorial sensitivity analysis on the harvest values to estimate the best combination.

Evaluation of management strategies

Once the ST determined the sensitivity and elasticity of the demographic parameters of the CNP WB population, we tested the effectiveness of reducing supplementary food availability and increasing selective harvest on modifying the variables selected by the sensitivity analyses in the future scenario. We did not evaluate the effectiveness of fertility control because the ST results of this strategy revealed a low effect on the variation in the projected population size. The output of each strategy was measured as the probability (PVA parameter “extinction probability”) of reaching the target population value and as the resulting WB population, both at the end of the future scenario period (25 years). The target population size (“extinction”) was set at 500 WB, half the theoretical natural carrying capacity of CNP (1,000 WB (Rosell et al., 2001)), since this 50% value maximizes recruitment (Mills, 2013). WB is a native species in the CNP and the aim is not eradicating this species from the CNP but maintaining the population below ‘threshold’ levels not causing negative impacts in the ecosystem (Massei & Genov, 2004).

We modeled the decrease of CNP HPT for WB through supplementary feeding reduction (Bieber & Ruf, 2005; Geisser & Reyer, 2004, 2005; Massei et al., 2011) from the current estimated HPT value of 3,000 to the target value of 1,500, assuming a minimum supplementary food availability for 500 WB over the environmental carrying capacity (1,000 WB, (Rosell et al., 2001)). We modeled such a decrease at two different rates: an idealistic option, with a 15% annual decrease for 5 years, and a conservative option, with a 5% annual decrease for 15 years. Secondly, we modeled the effectiveness of selective harvest (Bieber & Ruf, 2005; Geisser & Reyer, 2004; Herrero et al., 2008; Servanty et al., 2011; Toïgo et al., 2008), focused on increasing harvest in the best combination of values for juveniles and yearlings of both sexes provided by the sensitivity test results. Finally, we also modeled the effectiveness of an integrated management plan including the combination of supplementary feeding reduction and selective harvest.

5.1.4. Results

The past scenario

The population model calculated a population of 1,560 (34.42 SE) WB in 2015, agreeing with the evolution of the CNP WB population estimated from hunting bags, from 165 WB in 2000 to 1,500 in 2015. The deterministic annual increase (r) in WB abundance calculated by VORTEX was 0.3723.

The future scenario

The VORTEX simulations predicted that under the current conditions the CNP WB population will increase an 11.5% (until 1,673individuals, 26.81 SE), with an 8% probability of decreasing below the target size (500 individuals). Increasing HPT (K value) to 6,400 produced a consequent progressive increase in the final population size up to a 120.3% (until 3,304 WB, 61.56 SE) while the probability of achieving the target population size decreased to 4% (Figure 3.2).

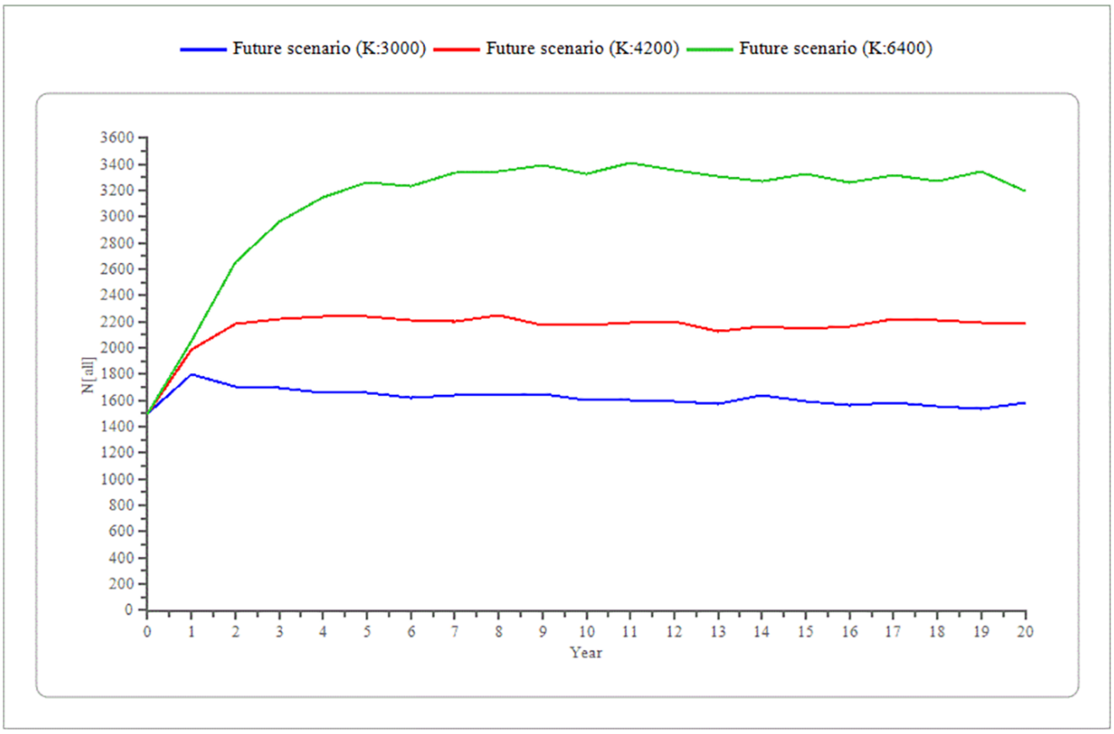


Figure 5.2. Predicted wild boar population trends. Future scenario results showed a progressive increase in the Collserola Natural Park final population size of: 1,673 wild boar for a K value (Hypothetical population threshold: Anthropogenic food resources availability) of 3,000, 2,281 WB for a K value of 4,200 and up to 3,304 WB for a K value of 6,400. Lines indicate SE.

Sensitivity analyses

The sensitivity analyses evidenced (Table 5.3, Figure 5.3 and 5.4) food availability as represented by HPT as the most influential parameter in population size (Figure S5.2), followed by the mortality rate of juvenile males and females, and the mortality rate of yearling males and females. The impact of adult male and female mortality on the variation in the CNP WB population size was not significant (Figure S5.3). Overall, the variations in female mortality rate had a stronger effect on population size than male mortality rate for all age-classes (Figure 5.4).

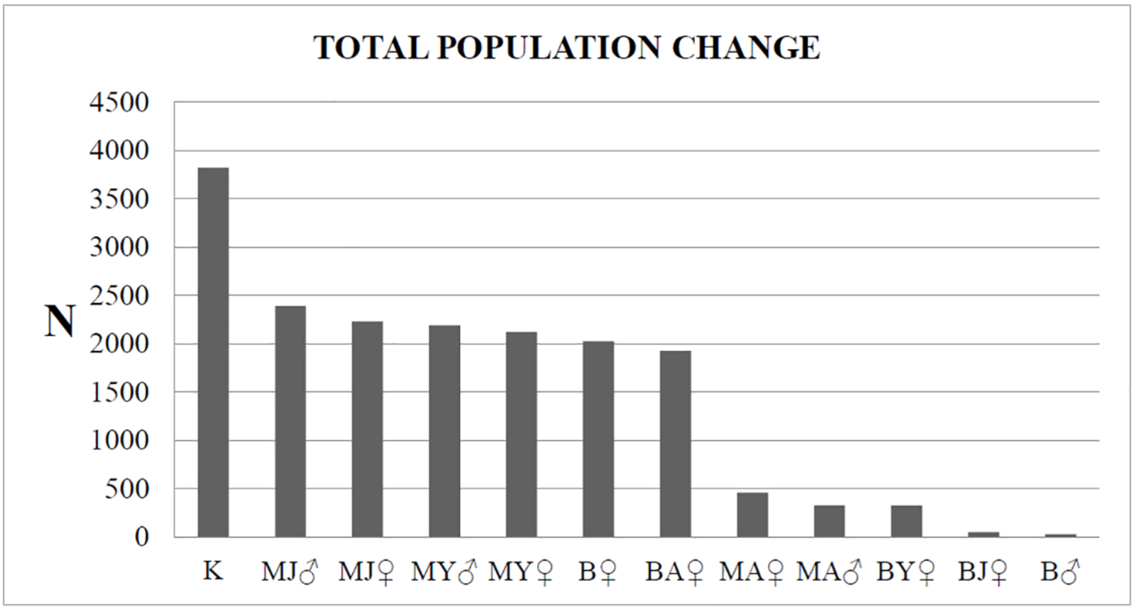


Figure 5.3. Impact of different parameters on wild boar population size according to the sensitivity tests. Total decrease (impact) in the wild boar population size of the Collserola Natural Park, Spain, for each parameter tested. K, Hypothetical population threshold: Anthropogenic food resources availability; M, Mortality; B, Breeding; J, Juveniles; Y, Yearling; A, Adults.

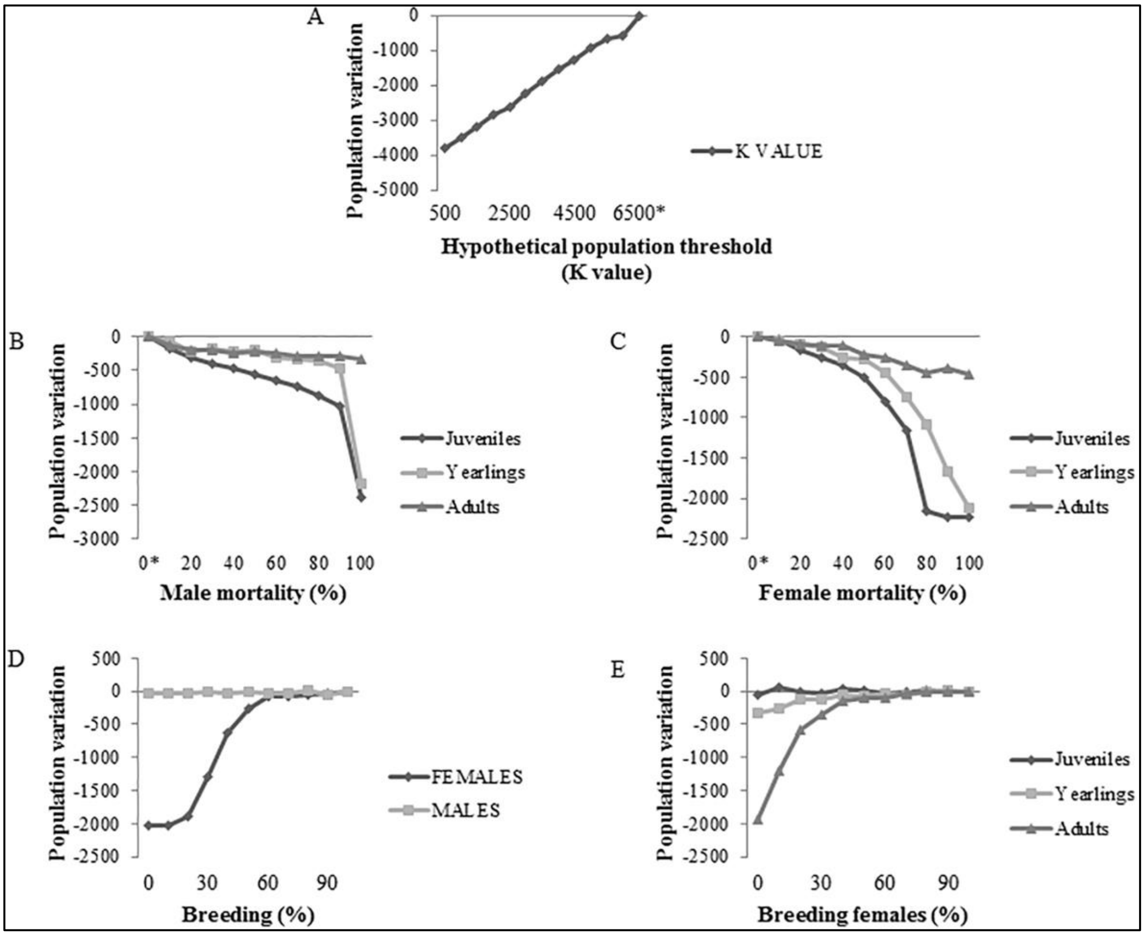


Figure 5.4. Effect of different parameters on wild boar population size according to the sensitivity tests. Wild boar population size of Collserola Natural Park, Spain, decrease for every 10% change of each of the parameters tested (A, Hypothetical population threshold: Anthropogenic food resources availability K value (Hypothetical population threshold: Anthropogenic food resources availability); B, male mortality; C, female mortality; D, breeding; E, breeding females). Breeding is the mean percentage of wild boar that breed in a given year (*, reference value).

Table 5.3. Sensitivity test results for the different parameters tested.

Parameter tested in the sensitivity test (minimum-maximum value)			**Relative population variation[a]**		**Variation between values** (number of individuals)
			At minimum value	**At maximum value**	
Hypothetical Population Threshold (500-6500)			-79.6%	+175.0%	3,820
Mortality	**Juvenile**	**Male**	-100.0%	+59.1%	2,387

(0-100%)		**Female**	-99.4%	+49.0%	2,226
	Yearling	**Male**	-100.0%	+47.9%	2,187
		Female	-98.5%	+42.5%	2,116
	Adult	**Male**	+25.0%	+46.7%	325
		Female	+14.1%	+44.6%	457
Breeding (0-100%)	**Males**		+27.5%	+29.4%	28
	Females	**All age-classes**	-100.0%	+34.9%	2,024
		Juvenile	+25.7%	+29.0%	49
		Yearling	+13.5%	+34.9%	320
		Adult	-93.7%	+34.7%	1,925

[a] The sign indicates the direction of the variation (+, increase; -, decrease)

Regarding reproduction, the variation in the percentage of reproductive females had a stronger impact on population size than for males (Table 5.3). Among females, the impact on WB population of the percentage of reproducing females increased with age. However, even though the variation in the predicted CNP WB population size due to the variation in the percentage of breeding females was high, only percentages of adult breeding females below 30% had an effect in achieving a significant reduction in CNP WB population size (Figure 5.4, S5.4 Figure).

The sensitivity analyses showed that a mortality rate between 40-60% for both juvenile and yearling WB, combined with a reduction of CNP HPT to a value of 1,500 WB, were the most effective measures to control and reduce the CNP WB population. Therefore, HPT and juvenile and yearling mortality were the variables selected by the model and consequently defined as target values for the management strategies (Table 5.4).

Table 5.4. Evaluation of the management strategies assessed in the model.

Management strategy	Effectiveness (success probability)	Years to reach target population size	Remaining abundance (N)
Decrease supplementary feeding	54[a]-56[b] %	6[a]-15[b]	626[a]-636[b]
Selective harvest	70 %	20	1651

Combined	100 %	5^{a}-10^{b}	<501

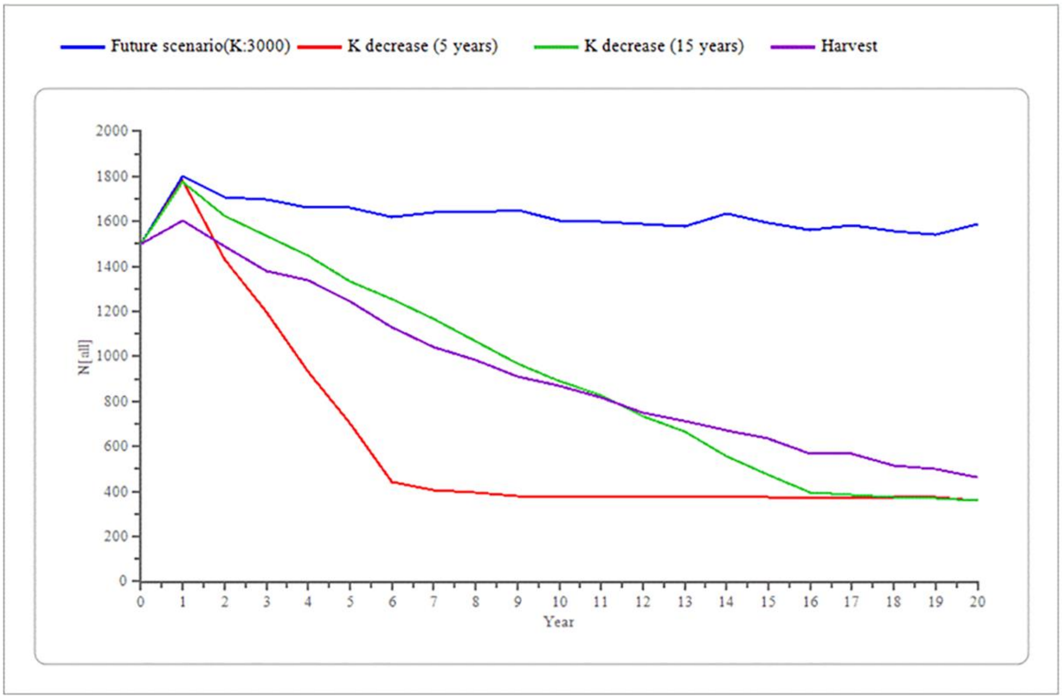
[a] Idealistic option (annual decrease of 15% during 5 years);

[b] Realistic option (annual decrease of 5% during 15 years).

Evaluation of management strategies

Decreasing the supplementary feeding had an 80% effectiveness to reach the target population value (fixed at 500 WB), with a 20% probability of decreasing the population a 58.6% (621 WB remaining) at the end of the modeled period for the idealistic decreasing rate option. The conservative decreasing rate option had an 86% effectiveness to reach the target population value, with a 14 % probability of achieving a population decrease of 59.1% (614 WB remaining) at the end of the modeled period (Table 5.4, Figure 5.5A). The sensitivity test in the harvest value of juveniles and yearlings selected 240 individuals, 60 from each sex within each age category, as the most efficient and effective value for the selective harvest strategy (Figure 5.6). This strategy had 72% effectiveness of reaching the target population value, but also a probability of 28% of a 7.4% increase in population size (1,611 WB) at the end of the modeled period (Figure 5.5A).

A



B

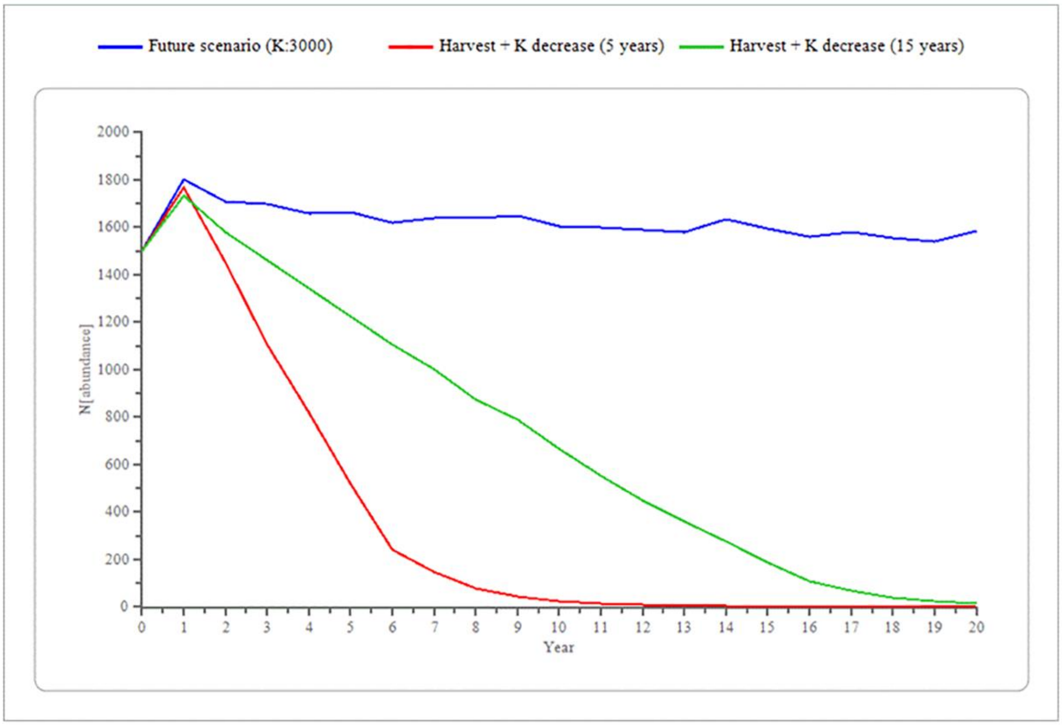


Figure 5.5. Predicted wild boar population trend under different management strategies. Results of testing the management strategies for the wild boar population of Collserola Natural Park, Spain, in the future scenario show different effectiveness, was a) 80% for the idealistic option (annual decrease of 15% during 5 years), 86% for the realistic option (annual decrease of 5% during 15 years) for the decrease of

anthropogenic food resources strategy and 72% for the Selective harvest strategy; and b) 100% for the Combined strategy.

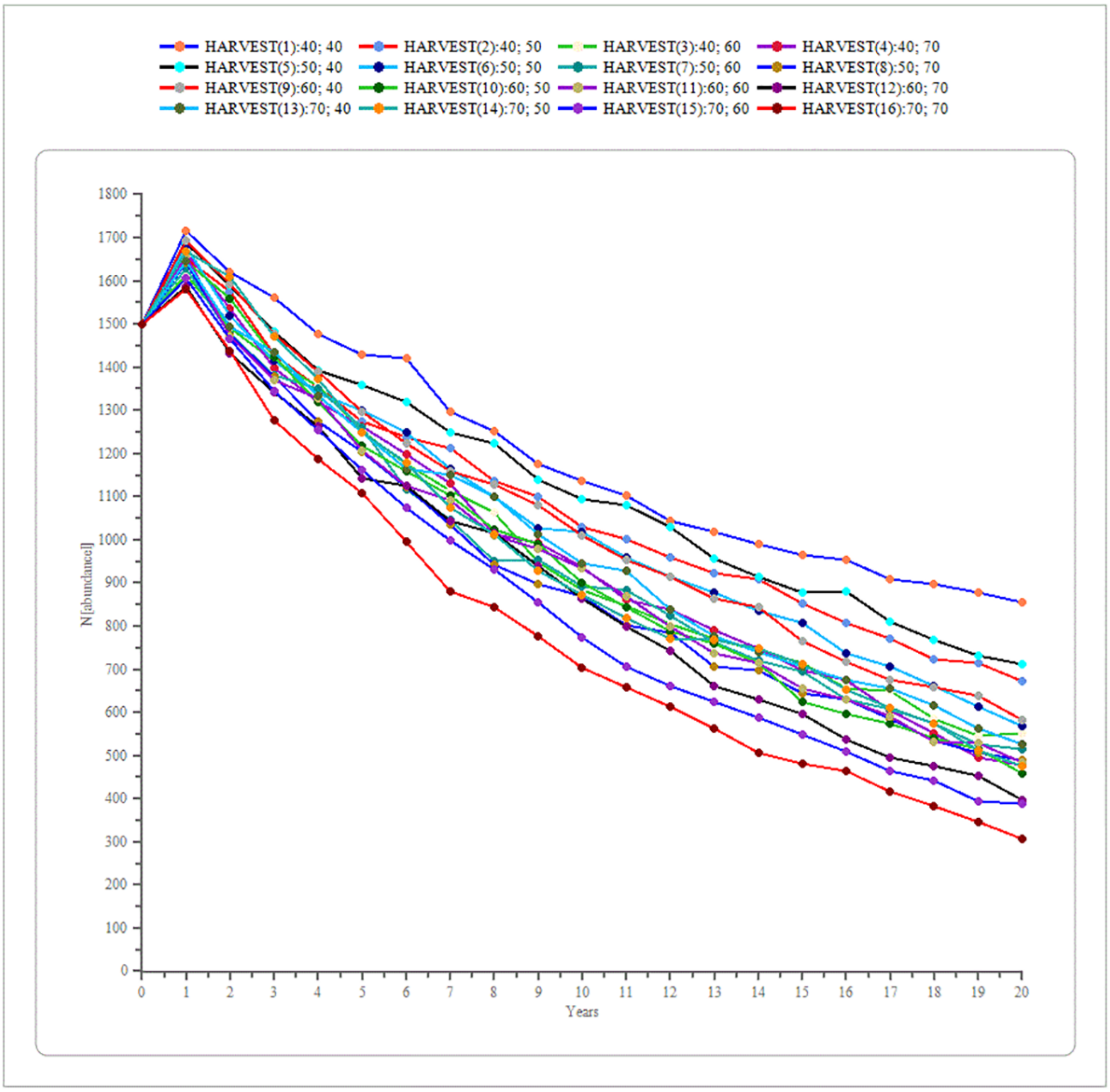


Figure 5.6. Effects of different harvest values. Sensitivity test outcome showed the relationship between wild boar population size trend and the different harvest values, from 40 to 70 juveniles and yearlings of each sex in the Collserola Natural Park, Spain.

When combining both strategies, the number of harvested WB necessary to control the population decreased (200 juveniles and yearling WB, 50 from each sex within each age category) while the effectiveness increased, achieving a 100% probability of reducing the population size below 500 WB by the end of the study period. The rate of decreasing supplementary feeding determined the time to reach this target population size, five years for the idealistic option and thirteen years for the conservative option (Table 5.4, Figure 5.5B).

5.1.5. Discussion

Our models established the combination of a reduction of supplementary feeding resources and the selective harvest of juveniles and yearlings as the most effective and efficient measures to control the CNP WB population and revert the increasing trend. The observed annual increase in WB abundance fell within the previous interval reported by (Choquenot & Ruscoe, 2003) (r: 0.211, 0.56 times lower) and (Hone, 2012) (r: 0.742, 1.99 times higher), and our predictive models pointed that under the current conditions and management the CNP WB population will continue to increase. Since most of the demographic values used in this study (Table 5.2) fall within or were obtained from the previously reported intervals for other WB populations thriving in Mediterranean environments (Focardi et al., 2008), the results and management applications obtained in our study could serve as a basis for other Mediterranean WB populations with supplementary feeding, either urban (e.g. rubbish, direct voluntary feeding, stray cat food) or agricultural (e. g. cereal, corn crops). However, since we used indices of relative abundance (hunting bags) producing high confidence intervals for WB population estimations (Table 5.1), our models would gain accuracy by using more reliable WB abundance data, like those obtained through population counts.

The supplementary anthropogenic food resources available to WB in the (peri)urban and urban areas surrounding and within the CNP has most probably increased CNP carrying capacity above the natural value (Cahill et al., 2012a; Cahill & Llimona, 2004). Summer is the period with highest mortality of WB in Mediterranean populations due to the natural scarcity of food and water (Massei & Genov, 1997), but supplementary feeding, irrigated green areas and artificial fountains provide food, water and thermoregulation for WB, thus avoiding the natural constraints of foraging on demographic effect (Choquenot & Ruscoe, 2003). In the CNP population, the incidences in urban areas are mostly caused by juveniles and females with piglets in good nutritional conditions in summer (Castillo-Contreras et al., 2018), suggesting that the availability of anthropogenic resources in (peri-)urban areas compensate the aforementioned natural environmental constraints. This artificial food supply and the consequent reduction in mortality makes difficult the estimation of the real carrying capacity of CNP by direct methods.

Mediterranean WB populations consist predominantly of juveniles and yearlings, with high reproductive rates and high mortality in the first year of life (Herrero et al., 2008).

WB have one of the highest fecundity rates among ungulates under good conditions (Bielby et al., 2007) and can even increase under strong hunting pressure, because of increased reproductive output of yearling females, which are recruited sooner and in a greater percentage (Boitani et al., 1985; Servanty et al., 2011). Therefore, Mediterranean WB populations are characterized by intense responses to food availability and weather conditions, resulting in sudden increases in numbers (Massei & Genov, 1997; Servanty et al., 2009). Under such conditions, generation time may be as low as two years, a value typically observed for rodents or passerine birds (Servanty et al., 2011). Population dynamics of WB population under favorable conditions seem rather typical for *r*, fast-life strategists or at an intermediate position along the capital–income continuum than for medium-sized ungulates (Bielby et al., 2007; Geisser & Reyer, 2005; Massei et al., 1996; Mills, 2013; Toïgo et al., 2008; Vetter et al., 2015). Altogether, the supplementary food available and the capability of WB of exploiting these resources explain the increasing trend observed in the CNP WB population, and consequently the relevance of reducing such food resources to revert this trend.

The current hunting management strategy has not achieved a reduction in the CNP WB population increase, but maintains the CNP WB population approximately half (i.e. 1,500 individuals) of the HPT value (i.e. 3,000 individuals). Traditional battues focus on adult WB whose mortality has little if any impact on the demography of the CNP WB population, whereas our models point juveniles and yearlings as the age classes to target in order to achieve a significant reduction in the CNP WB population. The effect of yearling male mortality was low, but distinguishing male and female juvenile and yearling WB is rarely feasible when hunting Mediterranean bush environments. These results agree with previously reported results in other WB populations, where the sensitivity of juveniles and yearlings were higher under good environmental conditions (Bieber & Ruf, 2005; Servanty et al., 2011; Toïgo et al., 2008), but are opposite to others where adult survival had the highest sensitivity in a growing population (Hone, 2012).This higher effect of juvenile and yearling mortality on population dynamics is likely related to the increased offspring production, piglet survival and population recruitment due to the overabundance of anthropogenic resources in CNP and the BMA.

Decreasing the percentage of breeding females did not seem a feasible target for reducing the CNP WB population, since it would be necessary to restrain the percentage of adult breeding females below 30% in order to appreciate significant effects on the population size. Future approaches to fertility control achieved through feeding may be able to target a much higher proportion of the population for a given effort, thus making fertility control a feasible option in restricted areas such as urban or protected areas (i.e. National parks).

When assessing the most efficient and effective measures to reduce the CNP WB population selected by the models, decreasing CNP supplementary anthropogenic resources modified both HPT (K value in VORTEX model) and mortality rates for all age classes (being therefore less specific). On the other hand, selective harvest had a strong effect on the mortality rate of specific age classes. Considering each management strategy separately, decreasing supplementary anthropogenic food resources has the strongest total effect, whereas selective harvesting is more effective and easier to implement, although reducing juvenile and yearling population might be more challenging than reducing adult WB population. However, the combination of both strategies reached 100% of effectiveness in achieving the management objectives (Table 5.3) and decreased the number of harvested WB required to control the population growth.

The agreement between the modeled and the estimated WB population trend from 2000 to 2015 indicated that the model was at least one of the possible explanations and that the carrying capacity, mortality and breeding rates used were reasonable. Our study showed the utility of PVA models as a species control management tool, for indirectly determining carrying capacity through the analysis of past scenarios, predicting population trend, and testing and targeting the sensitivity of biological variables and management strategies. This allows to design efficient and effective management plans prior to undertaking any action, increasing the effectiveness of management efforts through saving money and resources under the usually limited budgets. Though the final evaluation of the application of the results will require budgeting of the management actions, this was beyond the objective of the present study. That cost depends on the area and hence budget must be individually quantified for every particular context and management. PVA has also limitations, such as being usually focused on a single species, needing more data than other methods and, in many circumstances, the wide confidence limits of the estimates of extinction time produce meaningless results, unless used to compare the relative values of different management strategies (Akçakaya & Sjögren-Gulve, 2000; Benton & Grant, 1999).

5.1.6. Conclusions

The combination of decreasing carrying capacity by reducing supplementary food and focusing the harvest effort on the demographically most relevant age categories (i.e., juveniles and yearlings) revealed as the most efficient management strategy to control an increasing WB population in a Mediterranean (peri)urban environment with supplementary food over the natural resources. These strategies will probably be also the most efficient ones in other over supplemented increasing WB populations in similar situations, although studies should be carried out in a case by case basis in order to fine-tune the best management option and their specific efficacy and efficiency in each context.

Decreasing supplementary feeding involves natural, environmental and social factors. Management efforts should focus on (1) voluntary feeding control; (2) stray cat food; (3) waste collection; and (4) management of green areas in the CNP and its surroundings, including urban green spaces. Increasing night waits under special permits would allow targeting the vulnerable life stages, since they are more selective and efficient than traditional battues (Braga et al., 2010; Keuling et al., 2013). The capture of juveniles and yearlings WB using specially designed traps could also be an alternative option.

Our PVA allowed the prediction of the future trend of the CNP WB population under the current environmental conditions and management, validated by the agreement with the population trend observed in the past. Moreover, PVA also assessed the efficacy and efficiency of potential management strategies previously to their implementation, saving efforts and money by identifying those with more potential impact on the CNP WB population. This approach can be useful in other populations and scenarios not only for WB, but as a previous step before implementing management measures also for any other species.

5.1.7. Supporting information—Supplementary material

S5.1. Table. Vortex functions. Harvest and breeding functions used in the model of the Collserola Natural Park wild boar population.

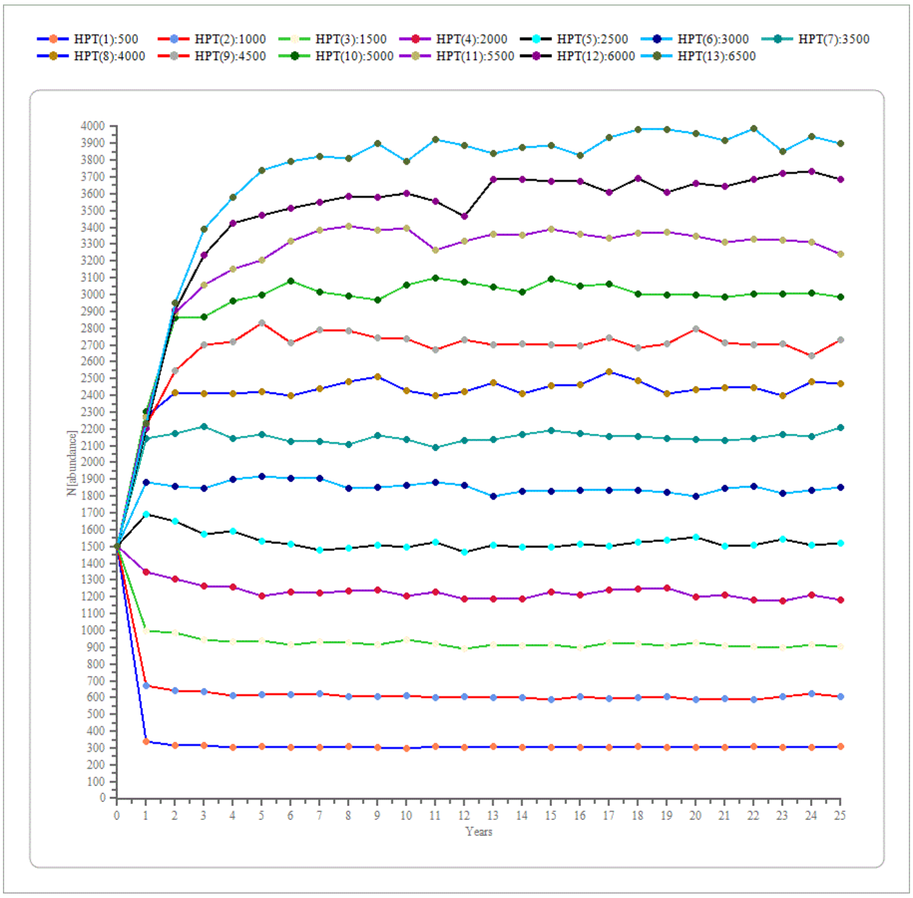
MODEL PARAMETER	FUNCTION
Harvest Past Scenario	=((Y<5)*((A<2)*((8,6*((10*N)/100)/100))+((A=2)+(A=3)+(A=4)+ (A=5)+(A=6)+(A=7))*((5,4*((10*N)/100)/100))))+ ((Y=5)+(Y=7)+(Y=8)+(Y=10))*((A<2)*((8,6*((15*N)/100)/100))+((A=2)+(A=3)+(A=4)+(A=5)+(A=6)+(A=7))*((5,4*((15*N)/100)/100)))+((Y=11)*((A<2)*((8,6*((20*N)/100)/100))+((A=2)+(A=3)+(A=4)+(A=5)+(A=6)+(A=7))*((5,4*((20*N)/100)/100))))+((Y=12)*((A<2)*((8,6*((25*N)/100)/100))+((A=2)+(A=3)+(A=4)+ (A=5)+(A=6)+(A=7))*((5,4*((25*N)/100)/100))))+ ((Y=13)*((A<2)*((8,6*((30*N)/100)/100))+((A=2)+(A=3)+(A=4)+ (A=5)+(A=6)+(A=7))*((5,4*((30*N)/100)/100))))+ ((Y=14)*((A<2)*((8,6*((50*N)/100)/100))+((A=2)+(A=3)+(A=4)+ (A=5)+(A=6)+(A=7))*((5,4*((50*N)/100)/100))))
Harvest Future Scenario	=((A<2)*((8,6*((30*N)/100)/100))+((A=2)+(A=3)+(A=4)+(A=5)+ (A=6)+(A=7))*((5,4*((30*N)/100)/100))
Female Reproduction	=(15*(A=0))+(60*(A=1))+(70*(A>1))

S5.2. Table. Hunting data. Wild boar captured, hunted or found dead from 2000 to 2015, used to calculate population and specific sex and age classes relative abundances and mortality rates.

Hunting season	Number of drive hunts	Mean drive hunt surface	Wild boar observed	Wild boar hunted	Drive hunt efficiency	Estimated wild boar populaton density	IC95%	Estimated number of wild boar
2000/2001	21	114,29	69	19	0,2754	2,06	2,580	165
2001/2002	25	84,75	103	35	0,3846	4,46	2,365	357
2002/2003	29	68,19	47	18	0,4500	2,39	2,196	193
2003/2004	27	70,96	80	27	0,3803	3,50	2,275	280
2004/2005	28	92,96	140	61	0,4357	7,24	2,234	579
2005/2006	-	-	-	-	-	-	-	-
2006/2007	13	111,69	102	26	0,2552	6,98	3,279	558
2007/2008	23	85,32	303	77	0,2541	8,61	2,543	689
2008/2009	-	-	-	-	-	-	-	-
2009/2010	22	87,43	116	50	0,4306	10,11	2,861	809
2010/2011	16	153,13	256	72	0,2813	10,26	2,663	821
2011/2012	18	156,01	287	84	0,2926	9,66	3,931	773
2012/2013	18	161,94	343	109	0,3182	13,13	3,299	1050
2013/2014	18	179,20	468	114	0,2434	9,49	2,036	760
2014/2015	17	175,00	213	75	0,3528	10,39	2,105	831
2015/2016	20	151,31	265	123	0,4645	18,75	2,544	1500

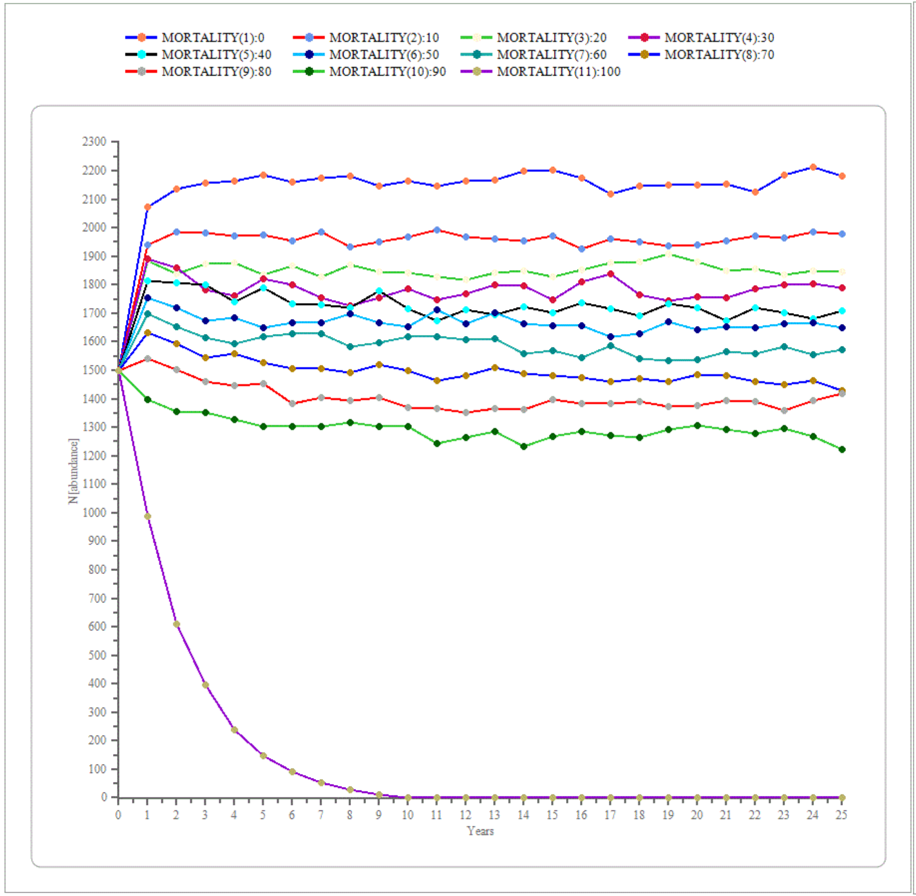
A) B)

S5.1. Figure. Urban wild boar. Wild boar population in the study area habituated to humans showing A) indirect and B) direct feeding from anthropogenic resources.

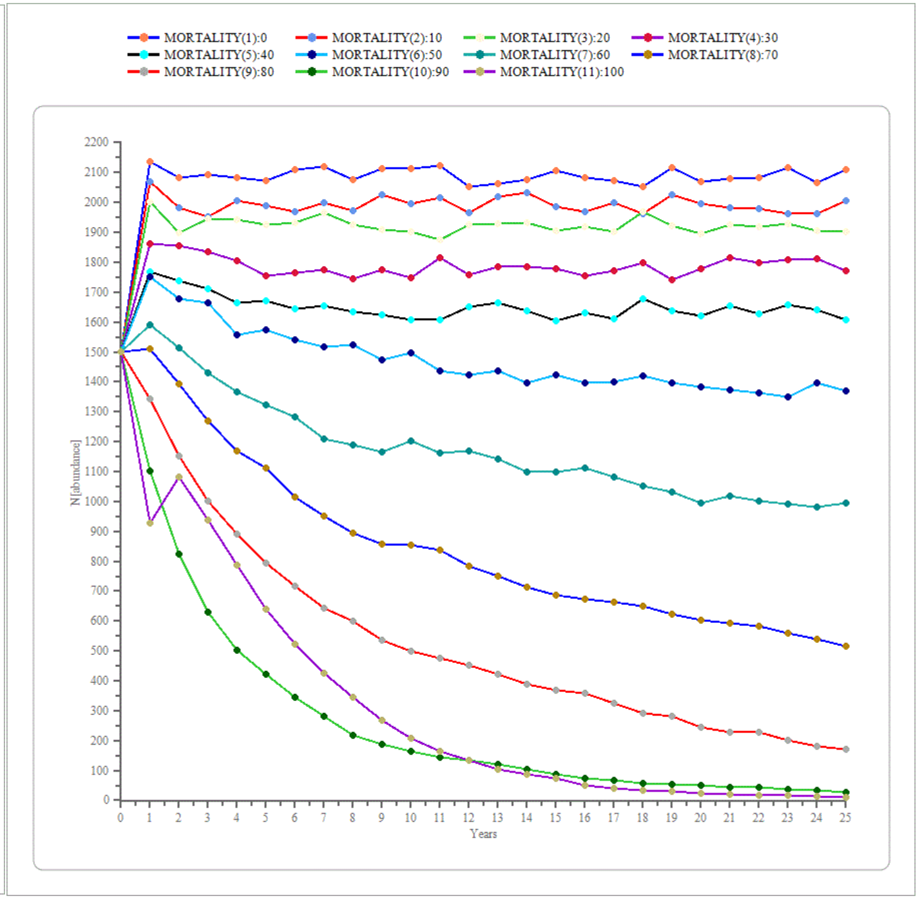


S5.2. Figure. Relationship between Hypothetical Population Threshold (HPT) and wild boar population trend. Sensitivity test outcome of the Hypothetical Population Threshold (HPT): Supplementary feeding availability (K value in VORTEX model), showed a total variation in the Collserola Natural Park wild boar population size of 3,820 individuals and an effect of 9.96%. Each line represents the population projection for the different HPT values (from 500 to 6500, increasing by 500).

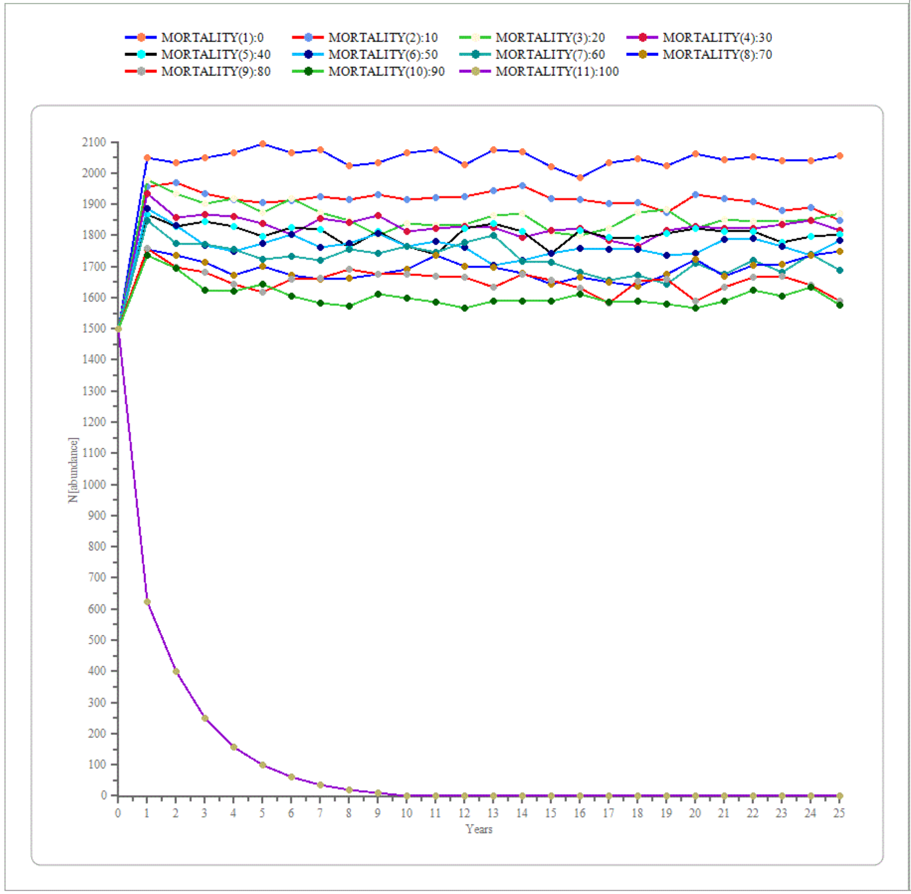
a)


MORTALITY(1):0
MORTALITY(2):10
MORTALITY(3):20
MORTALITY(4):30
MORTALITY(5):40
MORTALITY(6):50
MORTALITY(7):60
MORTALITY(8):70
MORTALITY(9):80
MORTALITY(10):90
MORTALITY(11):100
N[abundance]
Years

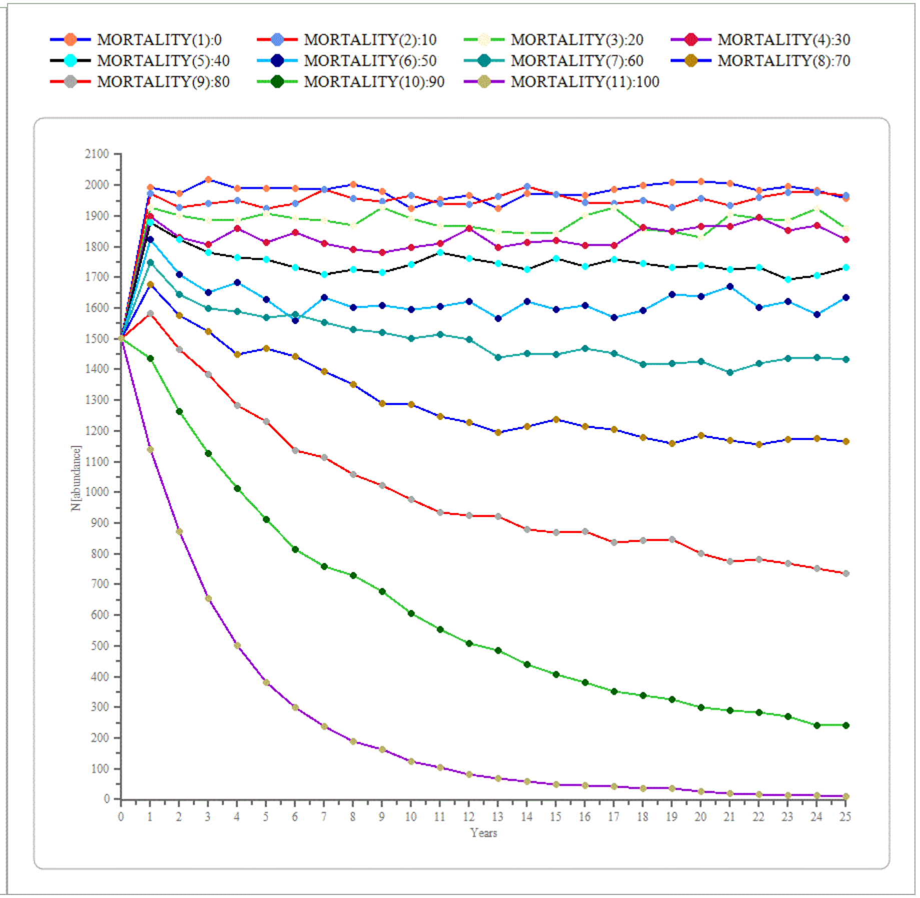
b)


MORTALITY(1):0
MORTALITY(2):10
MORTALITY(3):20
MORTALITY(4):30
MORTALITY(5):40
MORTALITY(6):50
MORTALITY(7):60
MORTALITY(8):70
MORTALITY(9):80
MORTALITY(10):90
MORTALITY(11):100
N[abundance]
Years

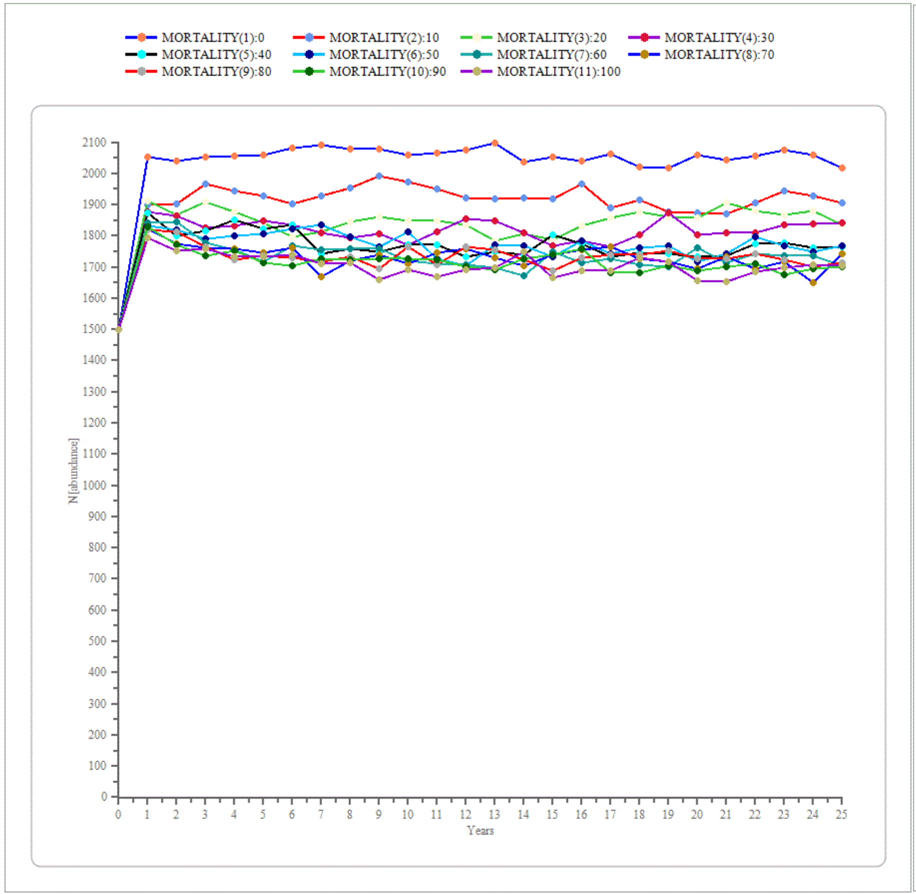
c)


MORTALITY(1):0
MORTALITY(2):10
MORTALITY(3):20
MORTALITY(4):30
MORTALITY(5):40
MORTALITY(6):50
MORTALITY(7):60
MORTALITY(8):70
MORTALITY(9):80
MORTALITY(10):90
MORTALITY(11):100
N[abundance]
Years

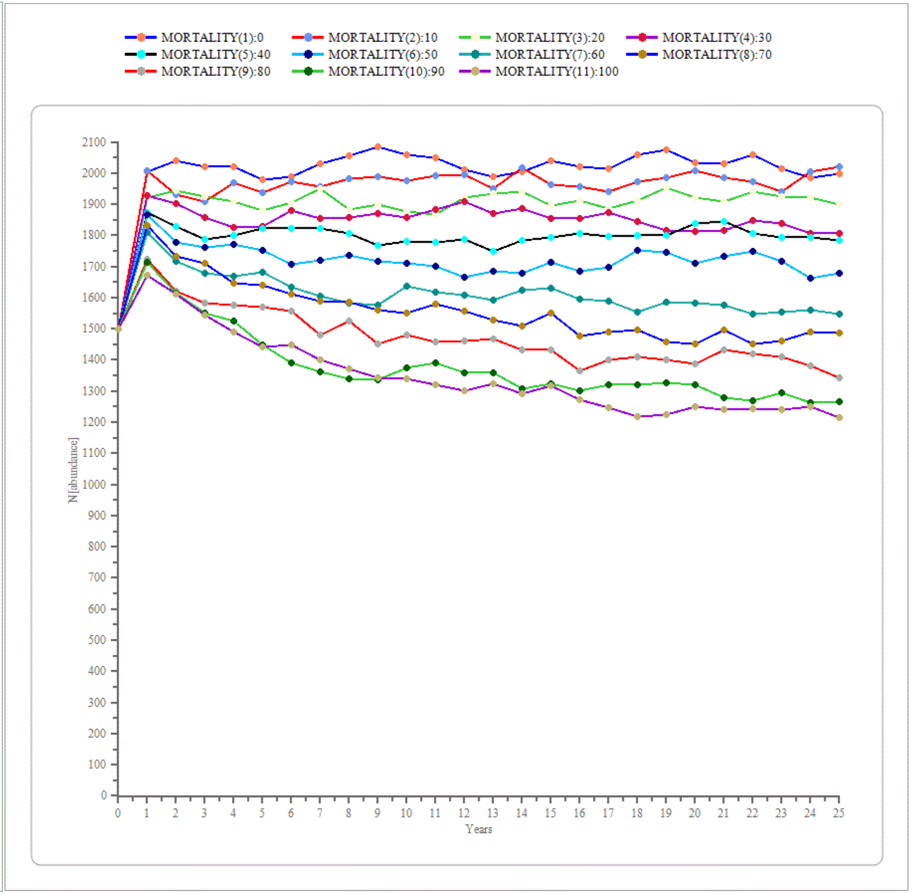
d)


MORTALITY(1):0
MORTALITY(2):10
MORTALITY(3):20
MORTALITY(4):30
MORTALITY(5):40
MORTALITY(6):50
MORTALITY(7):60
MORTALITY(8):70
MORTALITY(9):80
MORTALITY(10):90
MORTALITY(11):100
N[abundance]
Years

e)

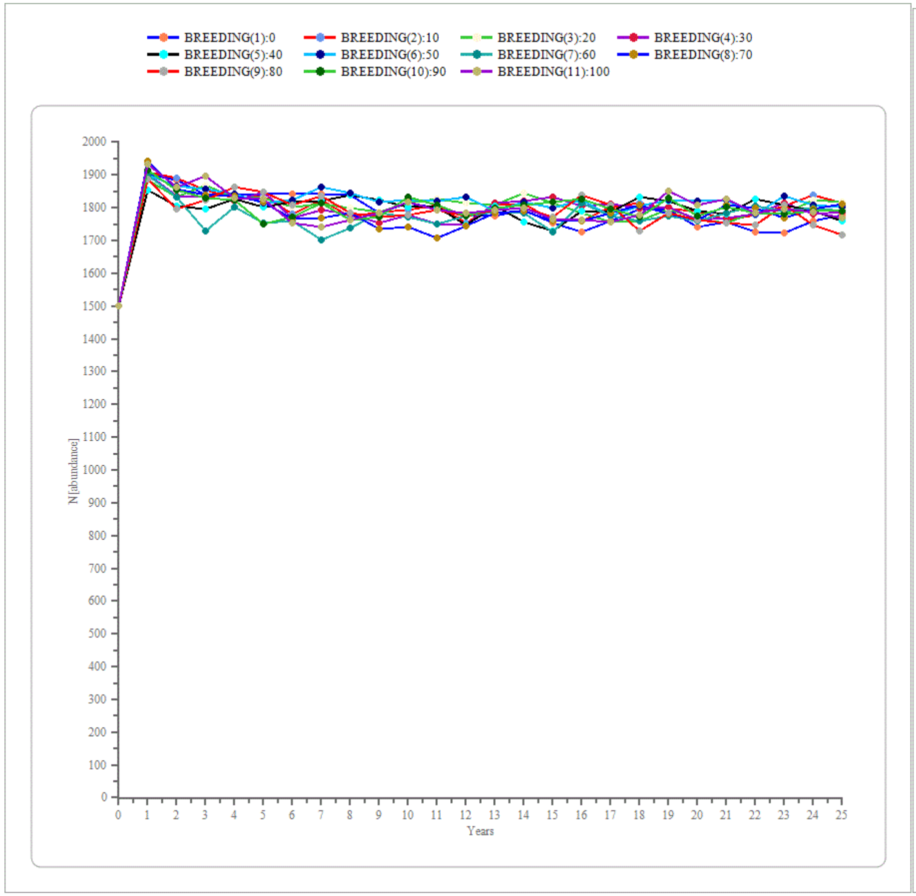


f)

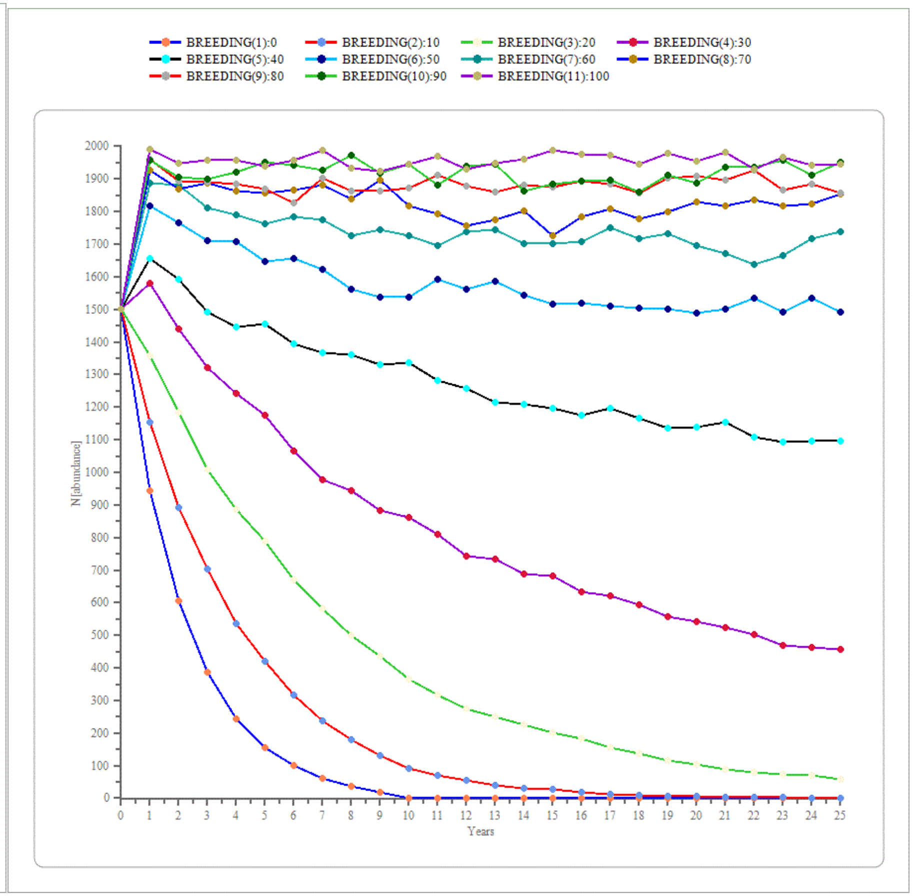


S5.3. Figure. Relationship between mortality and wild boar population trend. Sensitivity test outcome for the mortality rates of the wild boar population of Collserola Natural park (showed different values in variation in population size and effect for Juvenile a) males and b) females (2,000; 5.75%) , Yearling c) males and d) females, and Adult e) males and f) females. Each line represents the population projection for the different mortality values (from 0% to 100%, increasing by 10%).

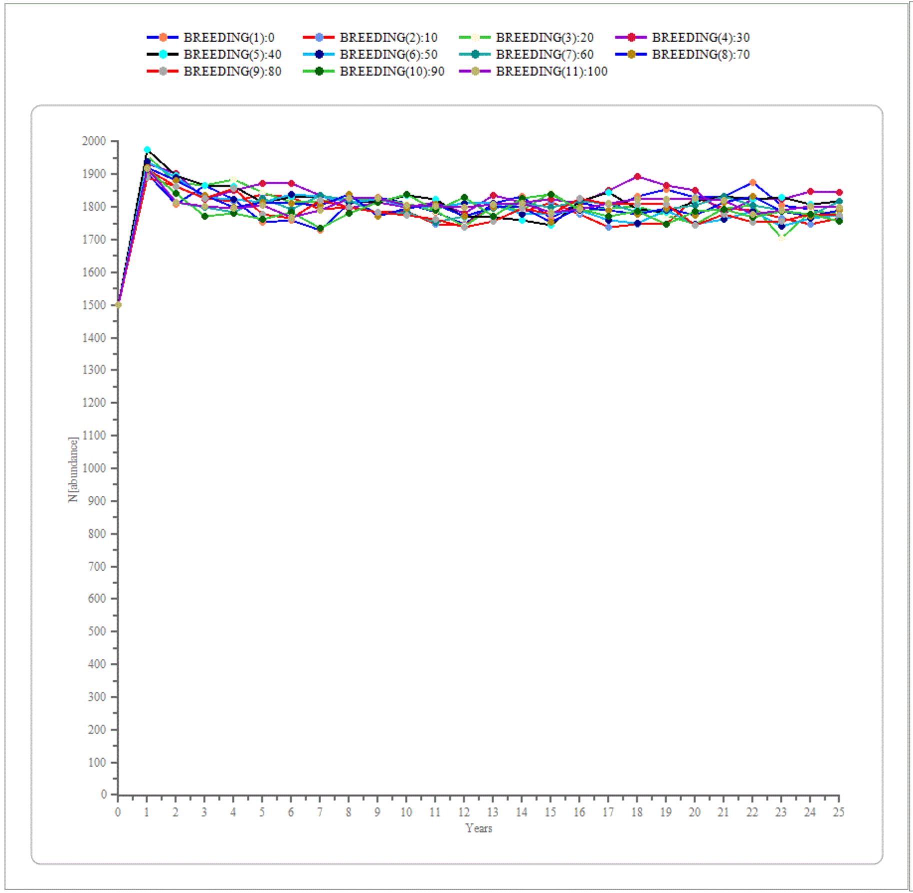
a)


BREEDING(1):0
BREEDING(2):10
BREEDING(3):20
BREEDING(4):30
BREEDING(5):40
BREEDING(6):50
BREEDING(7):60
BREEDING(8):70
BREEDING(9):80
BREEDING(10):90
BREEDING(11):100
N[abundance]
Years

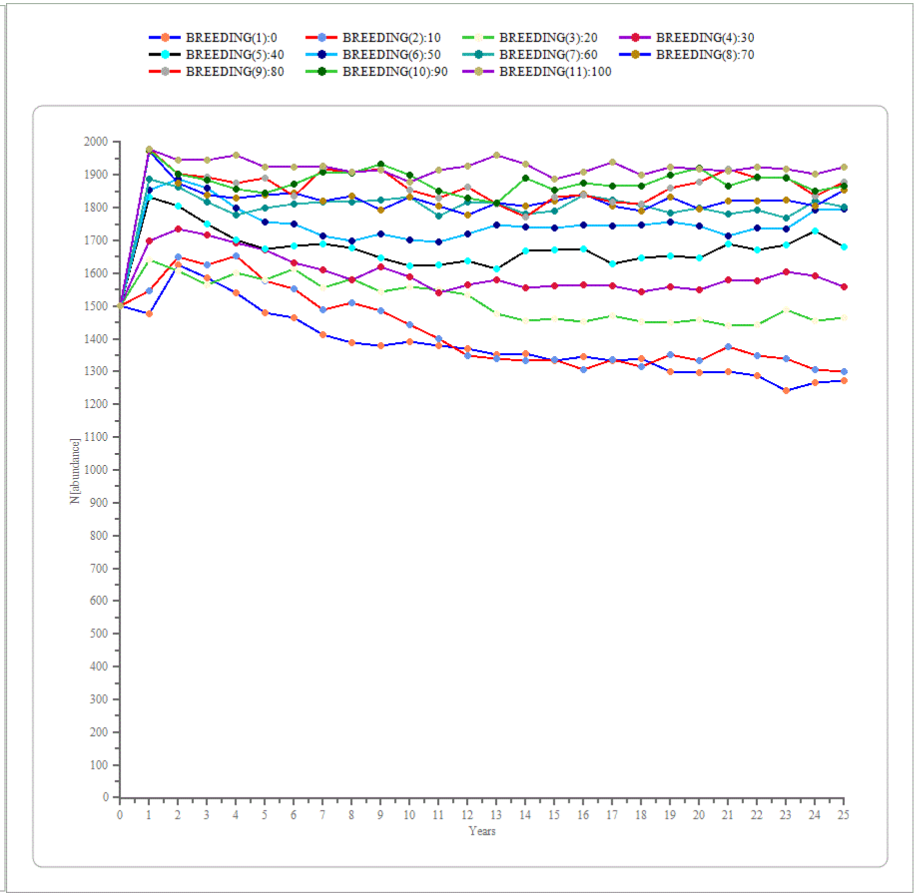
b)


BREEDING(1):0
BREEDING(2):10
BREEDING(3):20
BREEDING(4):30
BREEDING(5):40
BREEDING(6):50
BREEDING(7):60
BREEDING(8):70
BREEDING(9):80
BREEDING(10):90
BREEDING(11):100
N[abundance]
Years

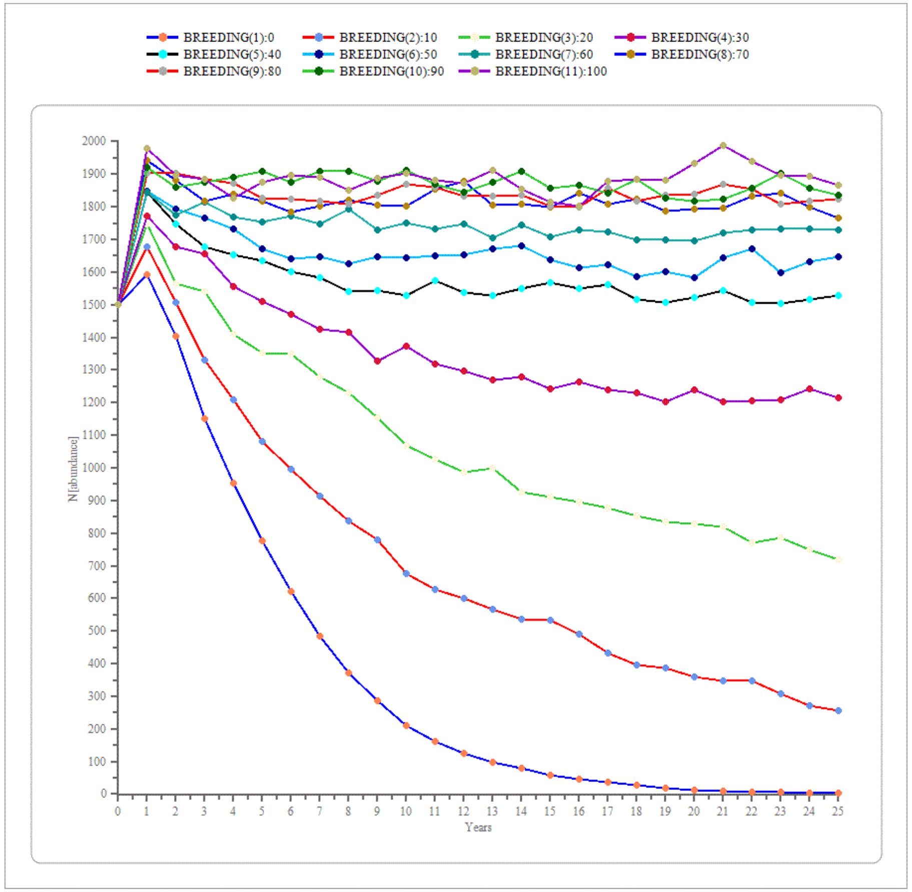
c)


BREEDING(1):0
BREEDING(2):10
BREEDING(3):20
BREEDING(4):30
BREEDING(5):40
BREEDING(6):50
BREEDING(7):60
BREEDING(8):70
BREEDING(9):80
BREEDING(10):90
BREEDING(11):100
N[abundance]
Years

d)


BREEDING(1):0
BREEDING(2):10
BREEDING(3):20
BREEDING(4):30
BREEDING(5):40
BREEDING(6):50
BREEDING(7):60
BREEDING(8):70
BREEDING(9):80
BREEDING(10):90
BREEDING(11):100
N[abundance]
Years

e)



S5.4. Figure. Relationship between fertility and wild boar population trend. Sensitivity test outcome for the fertility rates showed different values in variation in the Collserola Natural Park wild boar population size and effect for a) males and b) females, c) Juvenile females, d) Yearling females, and e) Adult females. Each line represents the population projection for the different breeding values (from 0% to 100%, increasing by 10%).

5.2 Study 2

Agent-Based Model of the wild boar-human interface in Barcelona, Spain.

5.2.1. Abstract

Synurbic species respond to global urbanization by gradually colonizing cities and using urban environments, where social and ecological (e.g. anthropogenic food resources and changes in the habitat) factors drive close human-wildlife interactions. The lack of management in the human-wildlife interactions leads to conflicts (e.g. damages, traffic accidents, attacks and disease transmission) which generate changes in animal population dynamics and an increase in public and private expenses. The aim of this study is to describe the BCNWB-prototype model, a spatially explicit incremental agent-based simulation model, where citizens and wild boar agents interact in recreated fine-scale GIS-based scenarios in Barcelona. The model was created using GAMA software and the results analyzed using QGIS and R software. The model seeks to simulate the dynamics of the current social-ecological system driving the use of the urban ecosystem by synurbic wild boar (*Sus scrofa*) and the human-wild boar interaction s in the (peri)urban area of Barcelona, Spain.

The results of the model showed high accuracy to predict the magnitude and location of wild boar movements (multiple-resolution-goodness-of-fit: 0.75) as compared to reports of wild boar observations in the city of Barcelona. The model predicted 115 attack events and 1442 direct feeding events during one year of simulation. The good performance of the model reflects the value of this prototype as predictive model to detect priority areas of human-wild boar interactions and conflicts. The model could be useful also to assess the cost-effectiveness of management strategies, as well as to evaluate the spread, transmission risks, and epidemiological implications for public health of different wild boar pathogens.

Keywords
Spatial-explicit simulation model, human-wildlife interaction, urban ecosystem, urban wild boar

5.2.2. Introduction

Urbanization continues expanding, with 56% of the human population currently living in cities (79.1% in developed countries) and it is predicted to be 68.4% by 2050 (86.6% in developed countries) (UN. 2018).

One response of wildlife to global urbanization is an increase of synurbization, where the new ecological niches are acceptable to some animal species (Luniak, 2004). In recent decades, wildlife usually associated with rural landscapes or undeveloped wilderness is gradually colonizing cities and thriving in urban environments (Ditchkoff et al., 2006). This leads to coexistence between wild animals and urban human society, creating opportunities and challenges for wildlife management in cities (Luniak, 2004; Patterson et al., 2003). Urbanization changes the social context in which wildlife management and decision-making occurs, with implications for the future of wildlife institutions and policies, where science has to be integrated (Patterson et al., 2003).

Wildlife presence in cities can have negative consequences (Ditchkoff et al., 2006) the close contact between wildlife and humans in urban environments has raised human-wildlife interactions (HWIs, defined as the spatial and temporal concurrence of human and wildlife activities where one part or both are affected (Decker et al., 2010; Patterson et al., 2003; Peterson et al., 2010)) and conflicts (Conejero et al., 2019). Since social and ecological factors are involved in HWIs, understanding the ecological role of wildlife in urban ecosystems is critical (L. W. Adams, 2005; Dearborn & Kark, 2010; Lischka et al., 2018; Magle et al., 2012).

As a generalist species, wild boar (WB) abundance has increased, spreading its distribution worldwide (Massei et al., 2011). The plastic behavior (Gamelon et al., 2013; Podgórski et al., 2013) and habituation to humans (allow WB to colonize and exploit a wide range of habitats, including (peri)urban environments (Cahill et al., 2012a; Castillo-Contreras et al., 2018; Stillfried, Gras, Börner, et al., 2017). In this environment, WB finds lack of natural predators and availability of anthropogenic food resources giving to urban populations an advantage over natural populations. These differences are especially relevant during the scarcity periods through the year, summer in Mediterranean areas, changing population dynamics by reducing mortality and increasing fertility and therefore boosting abundance ((Cahill et al., 2012a), Study 1) as described in other synurbic species (Luniak, 2004).

The presence of WB in urban environments attracted by anthropogenic food resources and the human habituation to the presence of WB in urban areas has exacerbated human-WB interactions and conflicts, such as damages in green areas and street furniture, traffic accidents, the risk of disease transmissions and attacks on people and pets (Conejero et al., 2019; Kotulski & Koenig, 2008); These conflicts have generated consequences in the social-ecological system of the human-wildlife interactions (Lischka et al., 2018). In the ecological system, it has produced changes in population dynamics, animal behavior and ecosystem imbalance due to overpopulation (Lischka et al., 2018; Tucker et al., 2020). In the social system, it has resulted in economic consequences such as the increase in public expenses related to restoring street furniture and green areas elements, capturing problematic individuals and police interventions, as well as private expenses related to green areas, plantations and facility restoration (Lischka et al., 2018). WB presence in urban areas also increases animal and public health concerns, such as disease transmission within the individuals of the same species and to humans and pets, traffic accidents or attacks to people or pets (Fernández-Aguilar et al., 2018; Meng et al., 2009; Wang et al., 2019). Other social consequences like fear to the presence of WB in the streets, conflicts among neighbors related to feeding behaviors, and animal welfare issues can also appear.

The city of Barcelona (BCN) with its metropolitan area (Barcelona Metropolitan area or BMA) containing the 80 km^2 Natura 2000 Collserola Natural Park (CNP), serves as an example of the challenge represented by the management of wild mammals in urban ecosystem. In recent years, part of the CNP WB population has become synurbic (Cahill et al., 2012a; Castillo-Contreras et al., 2018), therefore getting habituated to human presence and settling in the (peri)urban area of the BMA. Mostly from dusk to dawn, like in other European cities, (Podgórski et al., 2013; Stillfried, Gras, Börner, et al., 2017), the synurbic WB of the CNP population sneak into the urban area of BCN attracted by anthropogenic food resources (Castillo-Contreras et al., 2018).

Previous studies on the CNP WB population have evaluated the factors attracting WB into the urban area and the spatio-temporal preferences of these synurbic individuals inside the city (Castillo-Contreras et al., 2018), as well as the habituation of the BMA citizens to WB presence in urban areas (Conejero et al., 2019). Also, epidemiological studies of the BMA WB population have detected zoonotic diseases (Castillo-Contreras, 2019; Fernández-Aguilar et al., 2018; Navarro-Gonzalez et al., 2018; Wang et al., 2019). Regarding management, a population dynamics study and Population Viability Analysis (PVA) model with sensitivity tests (Study 1) pointed out reducing BMA WB abundance and anthropogenic food resource availability for synurbic wild boar as the best strategy, therefore decreasing human-WB interactions. This reduction of the WB abundance could be achieved through increased mortality, either hunting or using live-capture methods, which have been assessed from in terms of efficiency, feasibility and animal welfare (Torres-Blas et al., 2020).

However, the previous PVA model of the population (Study 1) did not include the spatial component. The use of spatially explicit agent-based models (ABM) (Bui et al., 2008; Heppenstall et al., 2012)) allows the inclusion of the spatial complexity of the social-ecological system to better evaluate eco-epidemiological scenarios and intervention strategies. The GAMA platform equipped with Geographic Information System (GIS) capacities (Taillandier et al., 2019) facilitates the integration of the city structure in a fine-scale resolution. By means of the ABM approach, a model can incorporate WB in the CNP population and citizens of the urban environment as individual agents, each involved in multiple activities and behaviors. As a result, ABM outcomes can identify areas with more WB presence and human activity and therefore more human-WB interaction risk.

The aim of this study is to present the BCNWB prototype, a spatially explicit ABM model, to study the synurbization of WB in the BMA, the use of the urban ecosystem by synurbic WB and the HWIs associated. This allows understanding the current social-ecological system of WB in the (peri)urban and urban areas of the BMA, by considering a diverse array of environmental, biological and social factors. The BCNWB prototype model aims to be used as foundational model for population studies and epidemiological risk assessment, as well as to inform the prioritization of mitigation and management measures previously proposed ((Massei et al., 2011), Study 1). It also allows the incorporation of high-resolution economical assessments.

5.2.3. Material and methods

5.2.3.1. Study area

The BMA is one of the largest European metropolitan areas, occupying 636 km^2 and populated by 3.24 million people (population density of 5,000 people per km^2) (Àrea Metropolitana de Barcelona, 2020). The Natura2000 Collserola Natural Park (CNP), included in the 110 km^2 Collserola massif, a Mediterranean hilly area with an altitude ranging from 60 to 512 meters, is located within the BMA. The study area (Figure 5.7) is composed by the CNP and the five out of the ten districts of the city of BCN directly contacting the CNP limit (see subsection scales in section a.2).

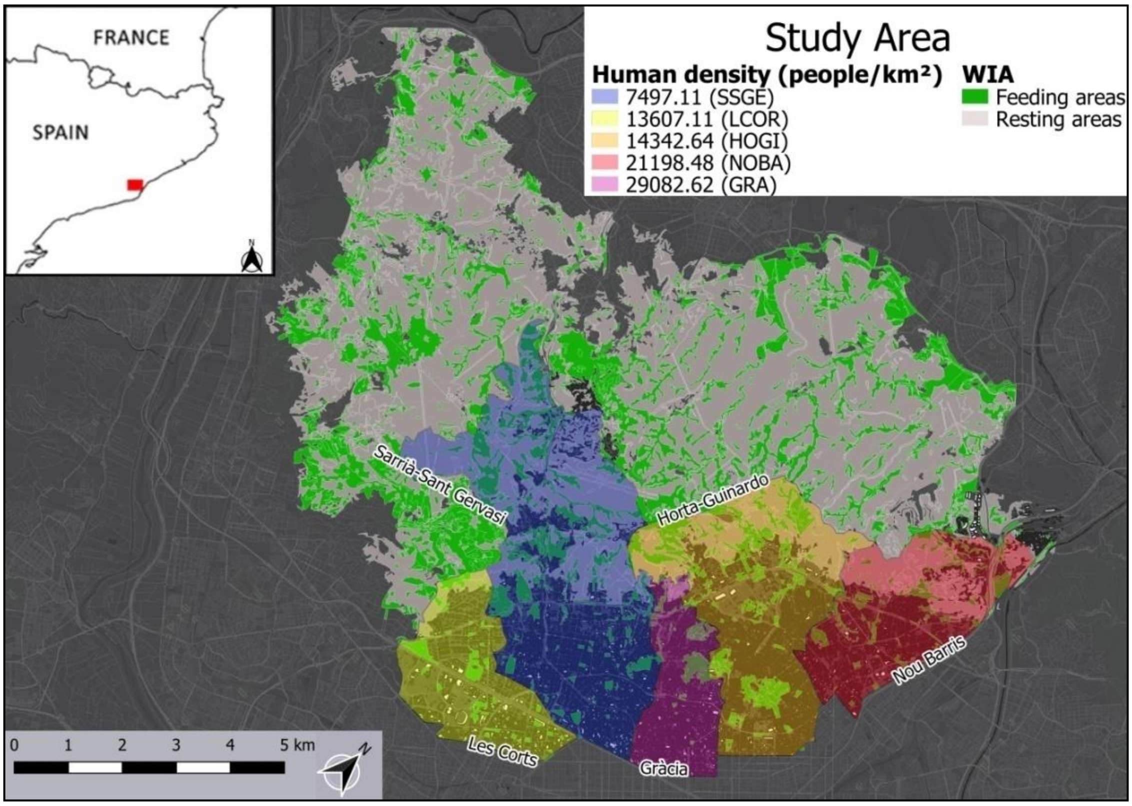


Figure 5.7. Study Area. Collserola Natural Park (CNP) and the five districts of Barcelona (LCOR, Les Corts; SSGE, Sarrià-Sant Gervasi; GRA, Gràcia; HOGI, Horta-Guinardó; and NOBA, Nou Barris), in contact with CNP included in the model. Population density and wild boar interaction areas (WIA, feeding and resting areas).

5.2.2.2. Model description

The description of the model follows the standard O.D.D. (Overview, Design concepts, Details) protocol (Grimm et al., 2010). The model was implemented in GAMA software, an AMB combined with GIS capabilities (Taillandier et al., 2019).

a) Overview

a.1) Purpose

The purpose of this study is to develop a base model, the BCNWB, which combines population dynamics, spatial and epidemiological processes with management decision-making in an agent-based framework. This model aims at studying and simulating the use of the urban ecosystem by synurbic WB and the derived human-WB interactions, as continuous processes in space and time, considering a natural ecosystem, the CNP, and an urban ecosystem, the city of BCN, Spain. The final objective is to develop predictive models to locate priority areas to mitigate human-WB interactions and conflicts, and to evaluate disease spread and transmission risk.

Therefore, the BCNWB model will help to understand the social-ecological system of the human-WB interactions in the urban area of BCN.

The management and epidemiological sub-models are not included in this study but they are planned to be included in future versions of the model to better support policy makers. However, we will outline future expansions over this model description.

a.2) Entities, state variables, and scales

- **Entities**

The model includes five main agents modeled from public available data: three non-mobile agents, (1) WB interaction areas (WIA); (2) buildings;(3) BMA road network; and two mobile agents, namely (4) the CNP and BCNWB; and (5) BCN citizens. A grid agent (100x100 m cell size) was included in the model, where each cell stored the spatially overlapping output data, subsequently exported as a vector map and used for validation and results. The integrated model has been subdivided, according to the social-ecological system created for HWIs (Lischka et al., 2018), into an ecological sub-model (E), comprising the environmental (EE) and the wild boar (EW) modules, and asocial (S) sub-model (Figure 5.8).

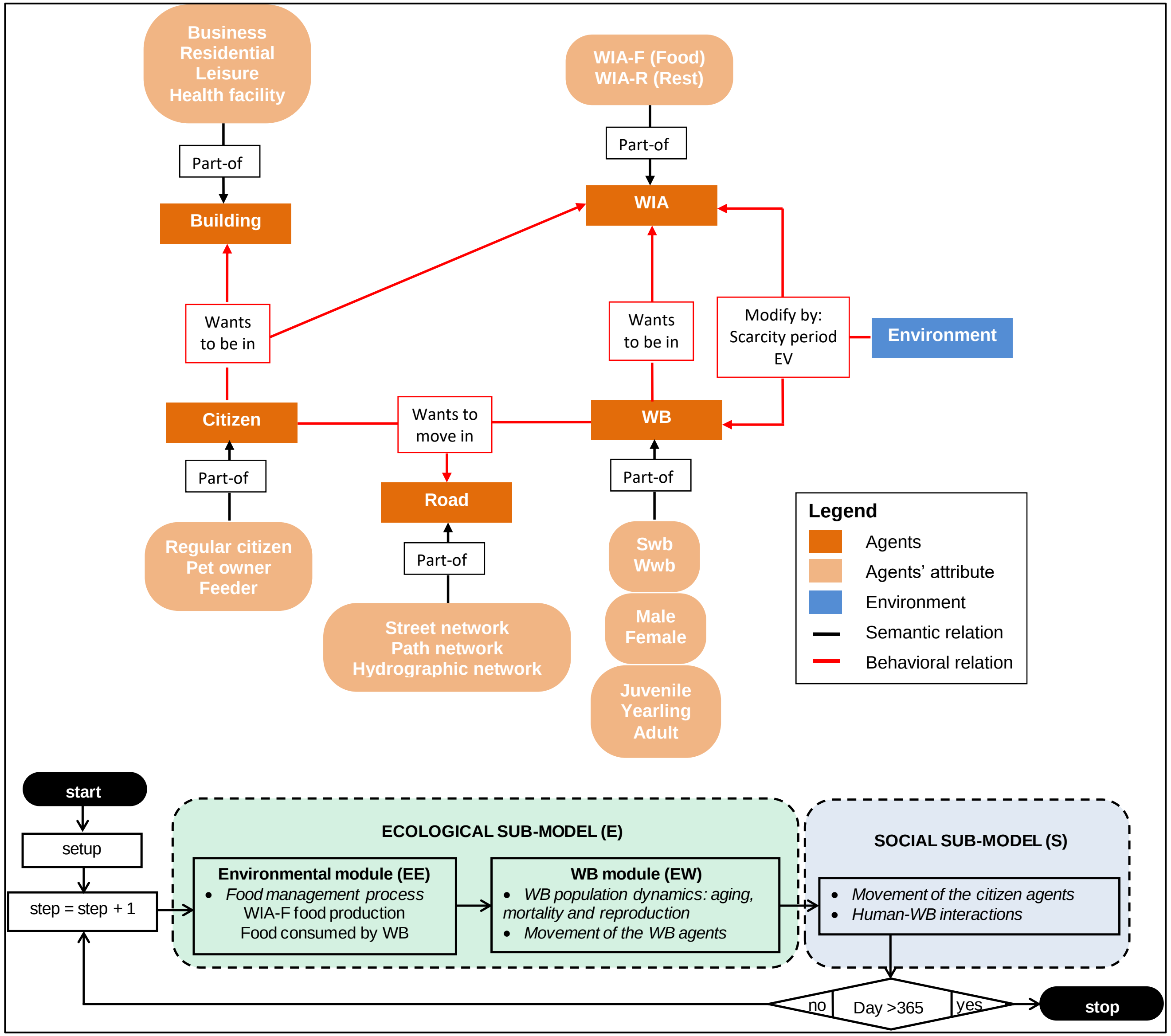


Figure 5.8. Up, Conceptual structure diagram of the BCNWB model; Down, Simplified flow chart diagram of the BCNWB model, with the ecological (E) sub-model containing both the environmental (EE) and wild boar (EW) modules and the social (S) sub-model.

The **EE module** is responsible for managing the environment of the simulation, composed by the natural (CNP) and the urban (BCN) ecosystems. Both ecosystems contain: (1) WIAs, composed by polygons used by WB as either feeding or resting areas or by citizens for outdoor activities;(2) buildings, composed by polygons where citizens stay working, resting or doing leisure activities (e.g. shopping, sports, activities,…) during specific hours of the day; and (3) road network, composed by polylines used by WB to move between WIAs and by citizens to move between buildings.

(1) The base for WIA in both ecosystems was the Land cover GIS layer for the CNP and green areas of BCN (Centre de Recerca Ecològica i AplicacionsForestals and Generalitat de Cataluña, 2019), including anthropogenic food resources used by synurbic WB inside the city of BCN (Recasens, 2017).

WIAs were divided according to the potential use by a WB. In the natural ecosystem, WIA-F (feeding area) polygons included evergreen oak (*Quercus ilex*), deciduous oak (*Q. cerrioides*) and croplands (herbaceous and woody). WIA-R (resting area) were composed by polygons with Mediterranean scrub and mixed woodland of Aleppo pine (*Pinus halepensis*).

Drought conditions during summer period increase soil compaction and therefore reduce rooting activity (Cahill et al., 2003). Scarcity in natural food can cause WB to increase their exploitation of anthropogenic food resources that remain available across the year (Castillo-Contreras et al., 2018). To capture these changes in natural food availability, a scarcity period from May to August was defined, where the value of FoodProduction and MaxFood (Table 5.5) of the WIA-F located in the natural ecosystem decreased 50%. Conversely, a scarcity period for the WIA-F located in the urban ecosystem was not defined, consistent with the irrigation of green areas and presence of accessible garbage (Castillo-Contreras et al., 2018).

Table 5.5. State variables included in the BCNWB prototype

Variable	Description	Type	Value	Reference
Environment				
Time	Simulated time	Date		
Date	Simulated date	Date		

CurrentHour	Current simulated hour	Int	0-23	
CurrentDay	Current simulated day	Int	1-30	
CurrentMonth	Current simulated month, 1-12	Int	1-12	
ScarcePeriod	Period when the MaxFood of each WIA is reduced to 50%	Bool	True from May to September	(Cahill et al., 2003)
ReproTime	Period when reproduction can occur	Bool	True from September to May	(Rosell et al., 2001)
(1) WIA				
ID	Identification of the WIA agent	Int		
Nature	Type: resting or feeding WIA	String	WIA-R and WIA-F	
GrowingPeriod	Period when the WIA-F agent produces food	Bool	True from CurrentHour: 8 to 20	
Food*	Quantity of food available in a WIA-F	Float	0-MaxFood	
MaxFood	Maximum quantity of food available in a WIA-F	Float	0.1-1	
FoodProd*	Quantity of food produced in each step	Float	Urban: rnd (0.009, 0.04)	
			Natural: rnd (0.006, 0.02)	
(2) Building agents				

Nature	Type of building	String	Working (business), resting (residences), leisure and health care	
(3) Road network agents				
ID	Identification of the building agent	Int		
Nature	Type of road network	String	Hydrological, path and street network	
(4) WB agents				
ID	Identification of the WB agent	Int		
AgeM	Age of the WB agent in months	Int	0-132	(Rosell et al., 2001)
MortalityRate*	Wb agent probability of dying for each sex and age class	Float	Table 5.6	
ReproductionRate*	Female WB agent probability to reproduce for each age class	Float	Table 5.6	
Pregnancy	Pregnant status of the female WB agents	Bool	True-False	
ReproductionDist	Distance where mating events occurs	Float	30 m	
GestationPeriod	Period when the female WB	Float	114 days	(Henry, 1968)

	agent Pregnancy status = True			
LitterSize*	Number of offspring	Int	1-6	(Rosell et al., 2001)
SexRatio*	Sex-ratio at birth of the WB agents initialized during the simulation	Float	0.5	(Rosell, 1998)
TimeForaging	Time when the WB agent starts the foraging activity	Int	CurrentHour: 20	
TimeHiding	Time when the WB agent stars the resting activity	Int	CurrentHour: 8	
Speed*	Normal speed of the WB agent according to sex and age class	Float	1-10 km/h	(Morelle et al., 2015)
DetectionDist	Distance at which the WB agents can detect food	Float	500 m	(Toger et al., 2018)
HabituationProb*	Probability that juvenile Wwb have to evolve to yearling Swb	Float	0.15	(Data gathered by the authors)
AggressiveState	Aggressive status of the Swb agents	Bool	True-False	
AggressiveProb*	Probability of an adult Swb to	Float	2.5% annual	((Fernández-Aguilar et al., 2018), surveys

	change to AggressiveState			(see Input data section c.2))
AggressionProb	Probability of an adult Swb to attack a citizen agent or pet?	Float	Table 5.6	
(5) BCN citizen agents				
Nb citizens	Initial number of citizen agents	Int	57,347	(Ajuntament de Barcelona, 2020)
Speed*	Normal speed of the citizen agent	Float	1-5 km/h	
TimeWork/ TimeNature*	Time when the citizen agent goes from the resting to the working assigned buildings or to the leisure destination, respectively	Int	1-12	
TimeRest*	Time when the citizen agent goes from the working to the resting assigned buildings	Int	16-23	
InteractionDist	Distance for human-wild boar interaction events to occur	Float	10 m	
FeedDist	Distance for feeding events to occur	Float	5.5 m	

FeedWbProb	Probability of a feeder citizen agent to feed a SWb agent	Float	0.37	(Surveys, (see Input data section c.2))

* State variables including random components

In the urban ecosystem, WIA-F polygons included the totality of green area surface located in the five districts considered in the model, in addition to anthropogenic food resources, such as stray cat colonies, unprotected waste containers and areas where citizens feed WB. In the boundary between CNP and BCN, a 100-meter wide strip was included in the urban ecosystem, with the same cover composition for WIA-F and WIA-R than in the natural ecosystem. WIAs are characterized by their color, namely green for WIA-F (color transparency indicates the Food value) and grey for WIA-R.

(2) Buildings were represented as a polygon vector layer containing the facilities of the urban ecosystem. Buildings were classified into business (office or factory, blue), residential (houses, yellow), leisure (shopping or sport, orange) and health facilities (hospitals, red).

(3) The road network was constructed as polylines vector layer containing the street, path and hydrographic networks of the BMA area. Non-urban WB could use the hydrographic (Castillo-Contreras et al., 2018; Sánchez-Montoya et al., 2016) and path networks to move between WIAs, but not the street network or the hydrographic network in the urban ecosystem, while synurbic WB could use the complete hydrographic network and also the path and street network. Citizens used the street and path networks but not the hydrographic network to move between buildings. The road network was characterized by colors, namely black, blue and brown for the street, hydrographic and path networks, respectively.

The **EW module** was responsible for managing the CNP and BCNWB population. To model the CNP WB agents, the population was sub-divided by: habituation state (non-urban (wild)wild boar, Wwb, 60%, and synurbic wild boar Swb, 40%); sex(males and females, 1:1); and age-class (juveniles, 0-1 year and yearlings, 1-2 years, 75%; and adults, >2years, 25%), having as a result 12 sub-CNP WB agent types. Population dynamics (PD) was also included in the model, i.e., the individuals changed their age-class, reproduced and died, according to the mortality and reproductive rates for each sex and age-class previously reported (Study 1).

(4) Wb were agents that moved between WIAs using the road network. Wb agents moved in the model according to the piloting navigation strategy (see the Basic principles section b.1), based on the activity pattern of WB in urban areas observed both by the authors (GPS collars, WB presence recorded by the local police and WB captures) and reported in literature (Cahill et al., 2003; Podgórski et al., 2013; Stillfried, Gras, Börner, et al., 2017) for both natural and urban areas. The main activities of WB agents were feeding in a WIA-F, resting in a WIA-R and moving between two WIA-For between a WIA-F and a WIA-R.

A 15% habituation probability (data gathered by the authors) was included in the model, capturing the habituation process of synurbic WB, where a proportion of Wwb juveniles became Swb when growing to yearlings. The attacks on humans and pets were also included in the model. In an attempt to capture this behavior, Swb agents had an aggressive status (true of false) driven by two probabilities: an aggressive probability, likelihood to become aggressive ((Fernández-Aguilar et al., 2018), surveys (see Input data section c.2.)) and only applicable to adult Swb older than three years, and an aggression probability, likelihood to attack a citizen or pet when a human-wild boar interaction takes place (surveys (see Input data section c.2.)). The aggression probability depended on the sub-type of citizen, being higher for feeders and lower for regular citizens and pet owners. The WB agents were characterized by color related to sex (male, blue; female, pink) and size related to age-class (juvenile, small; yearling, medium; adult, big).

The **S sub-model** was responsible for managing the human population of the city of BCN. (5) Citizens were agents that move between buildings using the road network. The citizens were also classified by behavior based on their habituation to the presence of WB and the possession of a pet. Hence, three citizen subtypes were defined: feeders (3.23%), who approach WB (by reducing their speed) and may feed them; regular citizens (67.7%) and pet owners (29.7%), who avoid contact with WB (by increasing their speed) (surveys (see Input data section c.2.))

Future versions of the model will add epidemiological and management sub-models within the ecological and social models, respectively.

- **State variables**

As the model is spatially explicit, each agent had a location attribute on a given time for the mobile agents, as well as a geometry, which can be either a point (WB and citizens), polylines (road network) or a polygon (WIA).

The stochastic biological variables, such as the proportion of breeding females, litter size, and mortality and synurbization rates, influence the population dynamics (PD) of the CNP WB. The processes associated were included in the model as empirically estimated probabilities (Table 5.6). Mortality rates were assumed to be sex- and age-dependent. Regarding reproduction the female population was exposed to pregnancy events from the age of six months, and fertility rates and litter size were assumed to depend on age only. Finally, synurbization probability was considered only for juveniles transitioning to yearling stage, with different habituation rate for each sex.

Future studies will add the WIA-F degradation rate, caused by WB due to the rooting activity in urban green areas and damages in street furniture, the WIA-F restoration and WIA-F elimination rate, capturing the management of green areas and street furniture by the BCN City Council.

- **Scales**

The study area (Figure 5.7) has 123.15 km^2,110 km^2 of natural ecosystems in the CNP and 13.15 km^2 of urban ecosystem in the city of BCN. The urban ecosystem is composed by the five districts of BCN in direct contact with the CNP, namely Les Corts (LCOR), surface 6.02 km^2 and population 81,974 inhabitants; Sarrià-Sant Gervasi (SSGE), surface 19.91 km^2 and population 149,260 inhabitants; Gràcia (GRA),surface 4.19 km^2 and population 121,798 inhabitants; Horta-Guinardó (HOGI), surface 11.96 km^2 and population 171,495 inhabitants; and Nou Barris (NOBA), surface 8.05 km^2 and population 170,669 inhabitants) (Barcelona City Council, 2019) in addition toa 100 meter-wide fringe of the boundary between both ecosystems, managed by the BCN City council. The simulations were launched from January 1st 2019 until December 31st 2019. Each step represented a one-hour time-frame, permitting the capture of the movement pattern of each individual during the simulation.

a.3) Process overview and scheduling

At each step of the simulation, the ecological sub-model was executed first, including the EE module creating the simulated environment and the EW module creating the PD and movement processes of the WB population. In the EE module, the amount of food available according to the food production for each WIA-F was updated. In the EW module, the schedule was based on WB PD and daily foraging-resting activity. First, PD demographic processes were executed, followed by the movement of the agents. The demographic events were scheduled in this order: births, age stage transition (aging), habituation, reproduction and deaths. The processes behind the events were included in the sub-model as described in section c.3. Then, the S sub-model was executed for the citizen movement, basing the schedule on human activity in the urban ecosystem (see sub-model section c.3.b).

- **Model verification, calibration and validation**

The model was verified, calibrated and validated (Heppenstall et al., 2012; Xiang et al., 2005). The verification process was performed in the initial steps of the model. Basic versions of the sub-models were evaluated independently, to verify the correct behavior of the modeled processes involved in the sub-models. When all the modeled processes in the sub-models were behaving as expecting, the input data were used to establish the values of the variables for the CNP WB population, thus calibrating the model to match the particular context of the study area. Prior to the final validation of the model, a validation of the calibrated PD process was performed, by comparison of the abundances and age-structure of the simulated and real population using a dataset of the years 2000-2015 (Study 1). After running the simulations, the grid agent with the model outputs (WB presence and attack and feeding events) was exported as a vector map. For qualitative validation of the model, the dataset of wild boar incidences (2014-2019) was included in the vector map and then, in order to visualize and analyze the results, vector and raster maps were created using the software QGIS v3.2 Bonn (Quantum GIS Development Team 2018) and used as independent validation data to assess the results of the model. The validation of the model was performed by means of multiple-resolution-goodness-of-fit, comparing the raster map resulting from the model with the raster map obtained with the actual WB presence in urban area (2014-2019). The analysis was carried out using R software (Version 4.0.3; R Core Team, 2020) with the mrgf function included in the spdynmod library (Martínez-López et al., 2015). The test fits for moving windows with increasing cell sizes from 1 to 113 and summarizes them into a weighted average (Costanza, 1989; Kuhnert et al., 2005). At last, the weighted average ratios of the predicted and the real WB presence were compared to assess the spatial relationship between them.

b) Design concepts

b.1) Basic principles

The WIA-F resource management was simulated under the basic assumptions that some WIA-F agents have greater MaxFood than others, accordingly with the type of resources contained, and the food production process of both natural and anthropogenic resources was active during daytime (see sub-model section c.3.a).

The movement of the WB agents during the daily foraging-resting activity was simulated with the basic assumption that WB use the piloting navigation strategy by allothetic navigation (Whishaw et al. 1999 and 2001). Wb rely on their olfactory ability, as the most developed sense in this species, for the perception of their environment, particularly relevant during foraging (Morelle et al., 2015; Suselbeek et al., 2012) and predator detection (Kuijper et al., 2014; Morelle et al., 2015). WB agents do not return to a WIA-F already visited in the same day and select the WIA-F closest to itself, not accordingly to its own preference of the type of food. The WB incidences data registered by the Barcelona police department in 2014-2019 and used to initialized the model (2010 data), to compared the generated annual urban activity pattern scenarios with the accumulated pattern (2014-2019 data) was considered to be a reliable proxy of WB presence in urban area.

The model also assumed that the citizen agent movement in the model recreated the human activity in the urban and natural ecosystems (Alfeo et al., 2019; Alonso et al., 2018; Grignard et al., 2018) of the BMA.

b.2) Emergence

The key outcomes of the model were the spatial activity patterns of the synurbic WB of the CNP population in the urban ecosystem of BCN, emerging from the piloting navigation strategy during the foraging activity in the natural and urban areas, driven by natural and anthropogenic food resources respectively. The PD of the WB population derives from the demographic events (births, deaths, etc.) of the population, but the occurrence of the events depends on the biological variables of the agents according to sex and age.

b.3) Adaptation

The habituation of WB to the urban ecosystem was a behavioral adaptive process in response to a habituation probability, which takes place over the simulation extent during the transition from juvenile to yearling age-states. Other behavioral adaptation of the Swb agent throughout the simulation was changes in the aggressive status and the aggression probability of a Swb. The attacking behavior of the Swb agents was adapted depending on external factors, such as the subtype of citizen (regular, pet owner or WB feeder). During the simulation, each WIA adapted to the influence of environmental conditions by changing their FoodProd and MaxFood available (Table 5.5). The environmental conditions modified the variables both intra-annually, due to a drought period of scarcity (see Entities section a.2), and inter-annually, due to the environmental variation (EV, see Stochasticity section b.5).

Future studies will add WIA adaptation to change, either modifying (reducing or increasing) the FoodProd and MaxFood due to degradation by WB and restoration by the City Council, or removing WIAs as a result of management practices.

b.4) Sensing, Interaction and Observation

The agents of the model have mainly direct interactions. WIA agents sense the WB agents located inside the polygon. The information is stored into a list and used to manage the food resources by the Environmental module (see sub-model section c.3.a). Building agents sense the citizens located inside the polygon, but in this model no interaction or observation was included. WB agents sense the WIA-F, whose value of the state variable Food is greater than 0.2 (within the 0.1 to 1 range), located within the detection distance of the agent.

The sole restriction of the model to the WB movement is that Wwb can only sense WIA-F located outside in the urban area and Swb can sense WIA-F located inside and outside the urban area but must select urban resources. Shortest path between WIA and between buildings is calculated by the corresponding WB and citizen agent as the path and distances are fixed and known. Swb and citizen agents can sense each other when they are located within the interaction distance. Particularly relevant for the present study are the human-wildlife interactions, principally those involving attack and feeding events. The information is stored into the grid agent, along with the Swb position when on the move, and used for results, validation and calibration.

Furthermore, the WB agents in the model have indirect interactions, the spatial competition among WB agents for the WIA-F resources due to the EE module in the piloting navigation strategy (see sub-model section c.3.a).

Future studies will add the use by the management sub-model of the data stored by the grid and WIA agents, to assess the prioritization of management strategies. In addition, the data stored by WB and citizen agents will be used by the epidemiological sub-model.

b.5) Stochasticity

In the Mediterranean area, the production and accessibility of natural food resources (eg. oak acorn) are variable across years. Inter-annually, spring weather conditions during flowering and acorn growth (Fernández-Martínez et al., 2012; Koenig et al., 2015) influence evergreen oak production ranging from 58 to 82% (Herrera et al., 1998) in the study area, with a full mast year *circa* every four years (Herrera et al., 1998; Rodríguez-Estévez et al., 2007). This environmental variation affects both WB reproduction and mortality (Geisser & Reyer, 2005; Servanty et al., 2009). Stochasticity due to EV was included in the model as a random inter-annual variation ranging +/-0.15 in mortality and reproductive rates, and in the FoodProd and MaxFood available in WIA-F (Table 5.6).

The EV also altered the habituation process in the model by modifying the habituation probability up to +/- 5%. In years with poor environmental conditions and consequently less availability of natural food resources, up to 15% of males and 13% females became synurbic, whereas in years with good environmental conditions, down to 5% of males and 3% of females shifted to habituated.

In an attempt to increase heterogeneity within the agent types, the speed and schedule of the mobile agents and the initial Food value in the WIA-F were randomly set according to reference values.

As a consequence of the stochastic nature of the model, each simulation was unique and irreproducible.

c) Details

c.1) Initialization

The BCNWB prototype started in January 1st 2019 at 10 AM, setting the initial state of WB agents in the model from the aforementioned input data. The simulation started by initializing buildings, roads and WIAs from their GIS shapefile, setting the physical ground for the mobile agents. The initial Food value was randomly assigned.

The prototype started with a population of 660 WB agents (average WB density of 6 WB/km^2 during 2015-2019), of which 348 were Wwb and 290Swb. 75% of the individuals were younger than 2 years. The Wwb agents were initialized in a random position inside aggregated polygons based on real hunting data (see Input data section c.2). Swb agents were created in a location recorded as a WB presence by the local police incidences dataset during 2010. The abundance and sex-age structure of the initial WB population in the model are based on empirically estimated population data of the real CNP WB population (Gonzalez-Crespo et al 2018).

After removing those citizens below three and above 85 years old due to restricted mobility, 10% of this value was included as mobile citizen agents in the model due to computational limitations. Thus, the prototype started with 57,347 citizen agents, randomly initialized inside a resting building. The number of citizen agents inhabiting each district in the urban area (Figure 5.9) was based on public demographic data (Ajuntament de Barcelona, 2020), and the proportion of those citizens working on each district was based on data available from surveys (see Input data section c.2).

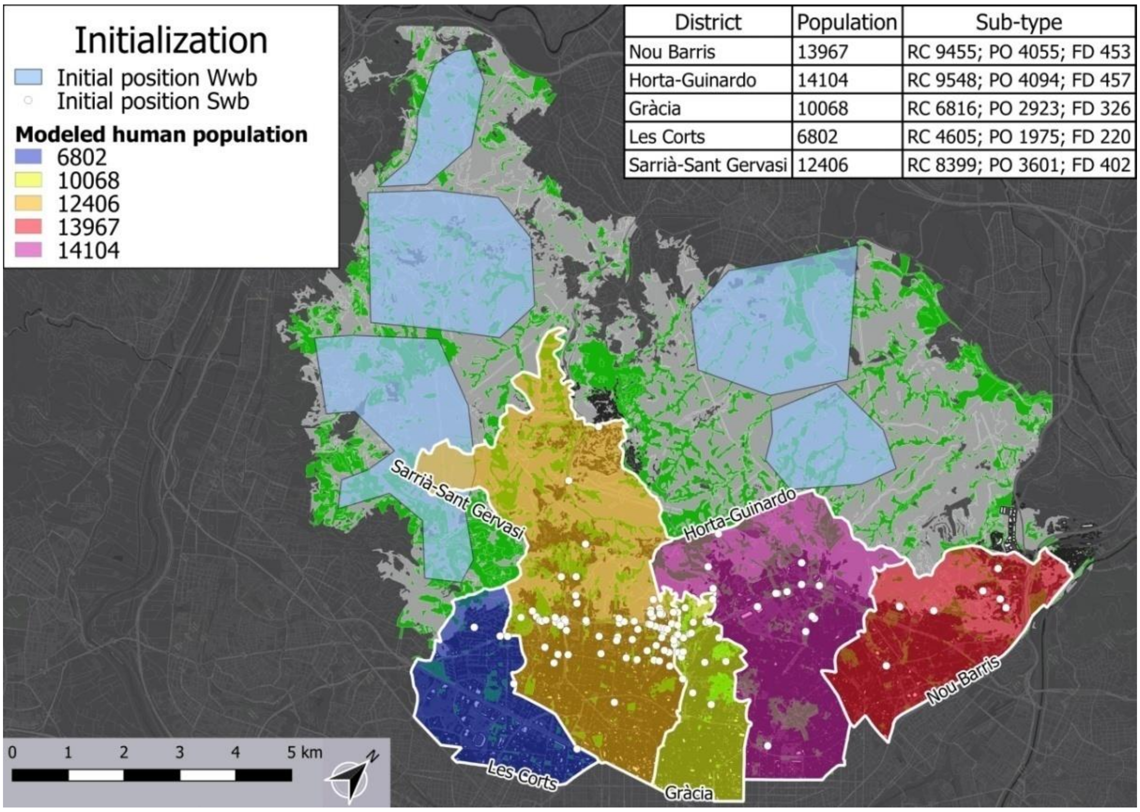


Figure 5.9. Initial location of the Wwb, non-urban wild boar and Swb, synurbic wild boar agents. Number of citizen agents by sub-type (RC, regular citizen; PO, pet owner; FD, feeder citizen), modeled in each district.

c.2) Input data

As the prototype model was spatially explicit, the input data used were also mainly spatially distributed and composed of geographical vector files in shapefile format (ESRI1998) and datasets. Prior to running the simulations, a preparation of the input data shapefiles was performed using QGIS software containing the definitions of the agents, represented as points, polylines and polygons, and the attribute tables.

Table 5.6. Input data and parameterization used for the BCNWB prototype

Variable	**Description**	**Type**	**Value**	**Reference**
(4) CNP WB agents				
Nbwb	Initial number of WB agents for each sex and age class	Swb Male Juvenile	90	(Study 1)
		Swb Male Yearling	32	
		Swb Male Adult	22	
		Swb Female Juvenile	91	
		Swb Female Yearling	35	
		Swb Female Adult	22	
		Wwb Male Juvenile	106	
		Wwb Male Yearling	39	
		Wwb Male Adult	26	
		Wwb Female Juvenile	108	
		Wwb Female Yearling	42	
		Wwb Female Adult	26	
MortalityRate*	WB agent annual	Male Juvenile	0.30	
		Male Yearling	0.43	

	probability to die for each sex and age class	Male Adult	0.35	
		Female Juvenile	0.29	
		Female Yearling	0.35	
		Female Adult	0.39	
ReproductionRate*	Female WB agent annual probability to reproduce for each age class	Female Juvenile	0.15	
		Female Yearling	0.60	
		Female Adult	0.70	
AggressionProb	Probability of an adult Swb to attack a citizen agent	To regular citizen	0.0126	(Surveys (see Input data section c.2))
		To pet owner	0.0379	
		To feeder citizen	0.0869	
(5) BCN citizen agents				
Nb citizens	Initial number of citizen agents for each sub-type	Regular citizen	38,823	(Surveys (see Input data section c.2))
		Pet owner	16,648	
		Feeder citizen	1,858	

* Variables modified by random EV (+/-0.15)

c.2.a) Environment of the simulation

- *Environmental variation*

The input data used to create stochasticity in the modeled processes due to EV was collected from data previously published by the authors (Study 1).

- *WIA, road network and building agents*

The vector layers used to initialize the road network and building agents were obtained from the Centro Nacional de Información Geográfica, (2018), containing topologic information at 1:25.000 scale. The attribute tables of the shapefiles prepared for the model contained the type of agent (e.g., river, path or street). The vector layer containing the land cover of the natural food resources and used to initialize the WIA agents was retrieved from the Centre de Recerca Ecològica i Aplicacions Forestals and Generalitat de Cataluña (2018). The attribute table of the original shapefile contained the land cover of each polygon. In an attempt to incorporate in the model, the availability of anthropogenic food resources within the urban area of BCN, during the preparation of the shapefile both direct and indirect data were used. Direct data included stray cat colonies (the location was provided by the BCN City Council) and waste containers used by WB and feeding areas (data gathered by the authors through transects). For the rest of the urban surface where direct data were not available, potential anthropogenic food resources were included from clusters of police incidences from 2011 to 2013, as well as randomly assigned in intersections in the urban roads, capturing the waste containers and street bins located in those locations. Altogether, 4,094 possible sources of anthropogenic food were included in the model from the aforementioned data, with an observed mean distance and the nearest neighbor index of 44.52 and 0.59, respectively. Then, the values of each type of natural and anthropogenic resources were transformed into numerical values of the variables MaXFood (ranging 0.1-1, according to the quantity of available food of their source type) (Cahill et al., 2012a; Castillo-Contreras et al., 2018) and FoodProd (ranging 0.0002-0.002, according to the type of resource).

c.2.b) Mobile agents

- *WB population dynamics (PD)*

All the data used in the PD process of the modeled WB agents (abundance, sex and age structure, mortality and fertility rates) were collected from data previously published by the authors (Study 1) and publicly available data (Departament d’Agricultura, Ramaderia, Pesca i Alimentació, Generalitat de Catalunya, 2019b)

- *WB agent movement*

Due to the importance in the study of the activity patterns of Swb in the urban ecosystem, data from both wild boar incidences in the urban area registered by the local police and hunting bag in CNP several sources were collected, in order to be used as input data for initialization, calibration and validation. The police incidence database recorded the citizen phone calls related to Swb presence in the urban area of BCN. This geolocated dataset is composed of an average of 600incidences per year, registered from 2010 to2019, and it is considered as a reliable proxy of the actual Swb presence in the urban area of Barcelona (Castillo-Contreras et al., 2018). This data set was used for calibration to set the initial location of Swb (2010) and validation (2014-2019). Hunting data from CNP consisted of the number and location of WB spotted and hunted in both drive hunts and night stalks carried out in the CNP for management purposes was used to set the initial location of the Wwb.

- *Citizen agents*

Citizen demographics were estimated from publicly available information (Ajuntament de Barcelona, 2018) Also, a dataset was constructed from surveys collected by the authors (from May 4th to July 23rd, 2018, eight trained pollsters interviewed 1,956 passers-by through the ten metropolitan districts of Barcelona). on citizen characteristics and past experiences with WB, including frequencies of contacts, feeding and attack events. This dataset was used to set the initial proportion of each citizen sub-types (Figure 5.9) living and working in the modeled districts, as well as to model the likelihood of a human-WB interaction after contact between citizen and Swb agents, such as feeding events and attack events, according to each citizen subtype.

c.3) Sub-models and modules

c.3.a) Ecological sub-model (E)

c.3.a.1) Environmental module (EE)

- *Food management process*

The EE executed the management process (Figure 5.10) of the available food in each WIA-F, where the value of the Food variable depended on the FoodProd and MaxFood variables assigned values. In each step of the simulation, the Food value increased by the FoodProd value (Table 5.5). The management process was only executed during daytime (8 AM to 8PM), and the maximum quantity of food available in a WIA-F was determined by the MaxFood value. When a WB agent was located within the polygon of a WIA-F, a quantity of food consumed was calculated in each step of the simulation, according to the age-stage of the WB agent and the surface of the WIA-F. Then this quantity consumed was deduced from the Food value.

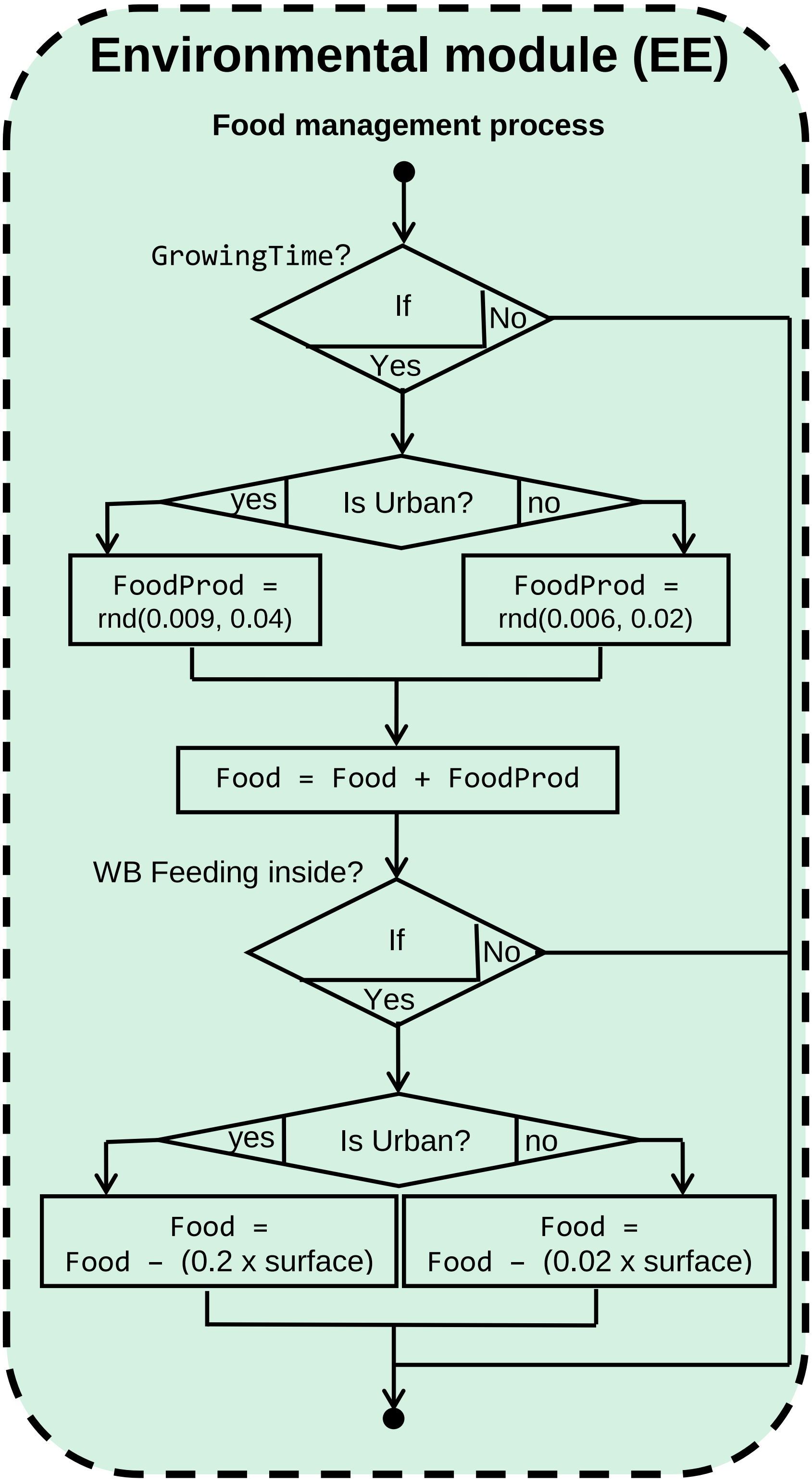


Figure 5.10. Flow chart diagram of the simulation process in the environmental (EE) module contained in the ecological (E) sub-model.

c.3.a.2) WB module (EW)

- *Population dynamics: aging, mortality and reproduction*

The age of the WB agents increased in each step of the simulation. When a WB agent arrived to 12 and 24 months, the type of WB changed from juvenile to yearling and to yearling to adult, respectively.

The death events of the WB agents were computed as a probability from the mortality variable set to each sex and age stage of agents.

In the simulation (Figure 5.11), the conditions needed for a reproduction event to occur depended on season; reproductive period; amating distance, capturing the need of a mating event between a male and a female WB agent; and a reproduction probability, capturing the fertility rates of the different age stages in female WB agents. When a male WB older than two years was located within the mating distance of a female WB, the reproduction probability assigned to the age stage of the female, determined if a pregnancy event took place. One hundred and fourteen days after a pregnancy event is scheduled, newborn juvenile WB were created in a number according to the litter size, each one with a sex randomly attributed from a 1:1 sex-ratio.

- *Movement of the WB agents*

WB were positioned on an initial location in a WIA-R. When the WB agent started to travel for feeding activity (Figure 5.11), chose as destination the closest WIA-F. WB agents were able to detect the WIA-F containing food >0.2 within a detection distance of 500 m (Toger et al., 2018). The WIA-F accomplishing the requirements were stored in a list and ordered according to the distance from the WB agent. Once arrived to the first WIA-F, the WB agent remained there a time proportionally related with the polygon area, until the amount of food was <0.1. Afterwards, it continued traveling always to the closest WIA-feeding, but never coming back during the same day to a WIA-F previously visited. When the agent had to travel back to the WIA-R, the WB chose as destination the closest WIA-R and started the trip. Once arrived to the WIA-R, the WB agent rested there until the next time to start the foraging activity again.

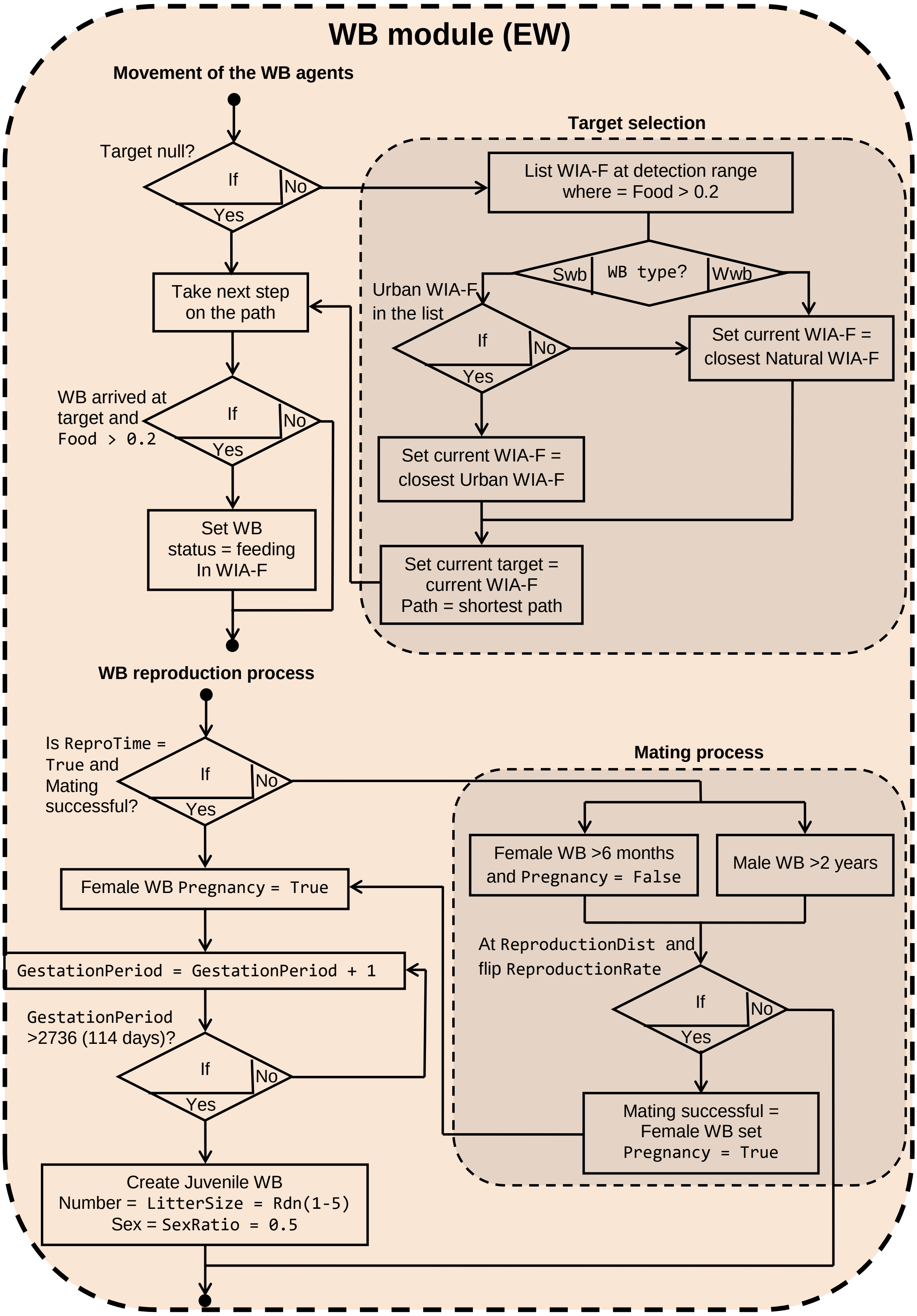


Figure 5.11. Flow chart diagram of the simulation process in the wild boar (EW) module contained in the ecological (E) sub-model.

c.3.b) Social sub-model (S)

- *Movement of the citizen agents*

Based on the human activity in the urban ecosystem (Alfeo et al., 2019; Alonso et al., 2018; Grignard et al., 2018), the citizen agents moved (Figure 5.12) on a working-resting activity during the week, between fixed working and resting buildings with an individual fixed schedule. During the weekend, with a variable schedule changing each day, the citizen agent randomly chose a leisure building, natural or green area where the agent spent a random time. According to the individual schedule of the citizen agent, when travelling (e.g., go to work, return home, etc.) the citizen chose a destination and followed the shortest path between buildings. The sub-model also included occasional appointments in health facilities, usually on a yearly basis or after a WB attack event. In an attempt to capture the use of different vehicles, when the distance to destination was higher than 2 km, the citizen agent increased the speed to 50 km/h.

- *Human-WB interactions*

Human-WB interactions (Figure 5.12) occurred both in the natural and urban ecosystems. While travelling, when a citizen was within the interaction distance from a Swb (10 meters, Table 5.5), a human-WB interaction could take place. When the citizen sub-type was a Feeder agent, a feeding event on Swb happened under the conditions defined by the feeding probability. In the event that an aggressive Swb found citizens, the aggression probability determined whether there was an attack. After the human-WB interaction, both the Swb and the citizen kept traveling.

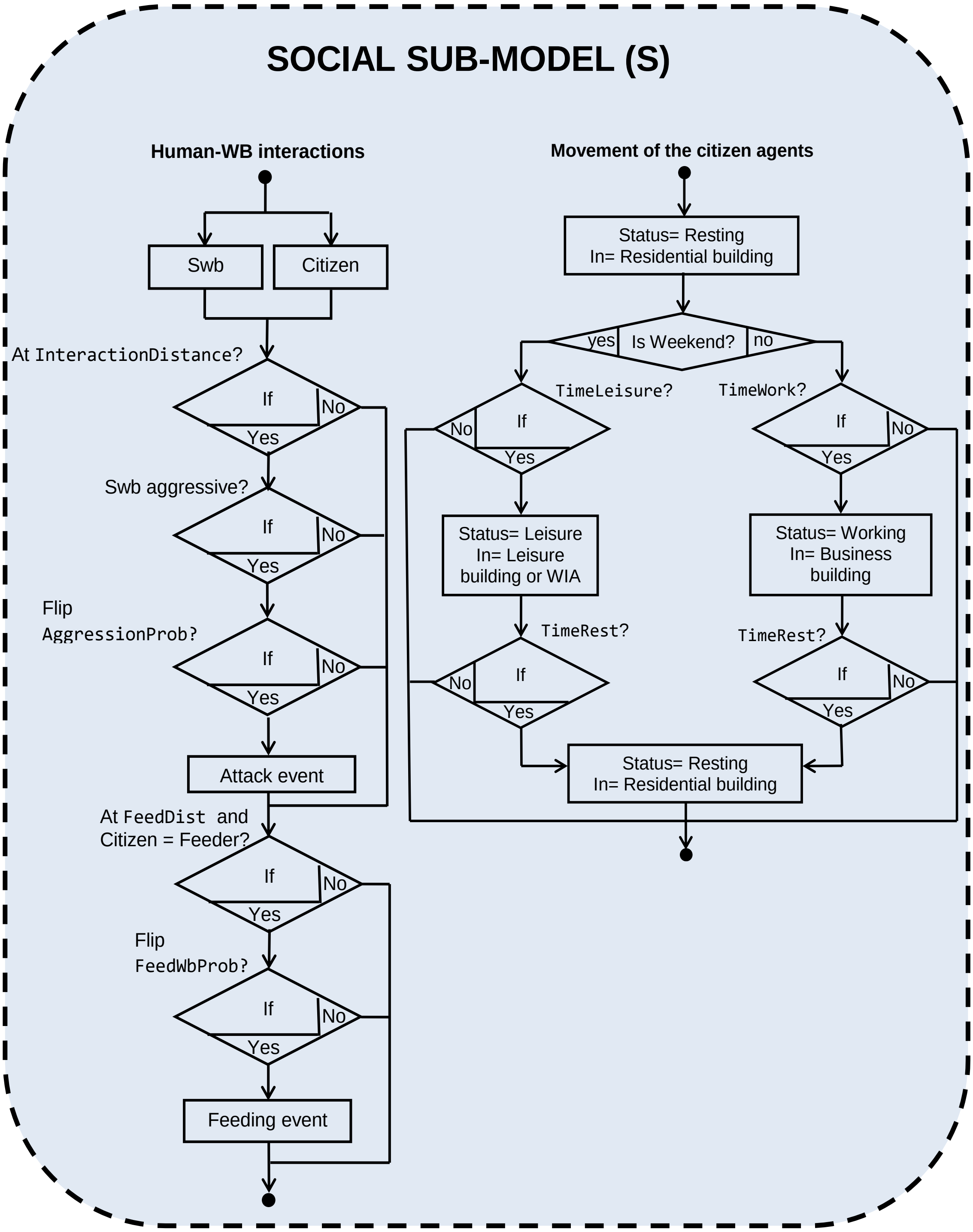


Figure 5.12. Flow chart diagram of the simulation process in the social (S) sub-model.

5.2.4. Model results and evaluation

Figure 5.13 shows the presence of WB in the urban districts of BCN in contact with CNP, as predicted by the BCNWB model and as registered by the Barcelona police department. The model was able to spatially simulate the effect of the social-ecological system of the human-WB interactions, in a timely and spatially manner during the study period, accounting for (1) the potential use of space in the urban ecosystem by Swb; (2) the differential effects of the exploitation of natural and anthropogenic food resources in the synurbization process; and (3) the WB PD in the natural and urban ecosystems. According to both the values simulated by the model and those registered by of the Barcelona police department (Figure 5.13), synurbic individuals of the CNP WB population infiltrate into the urban area of BCN during the daily foraging activity for anthropogenic food resources, creating the conditions for human-WB interactions.

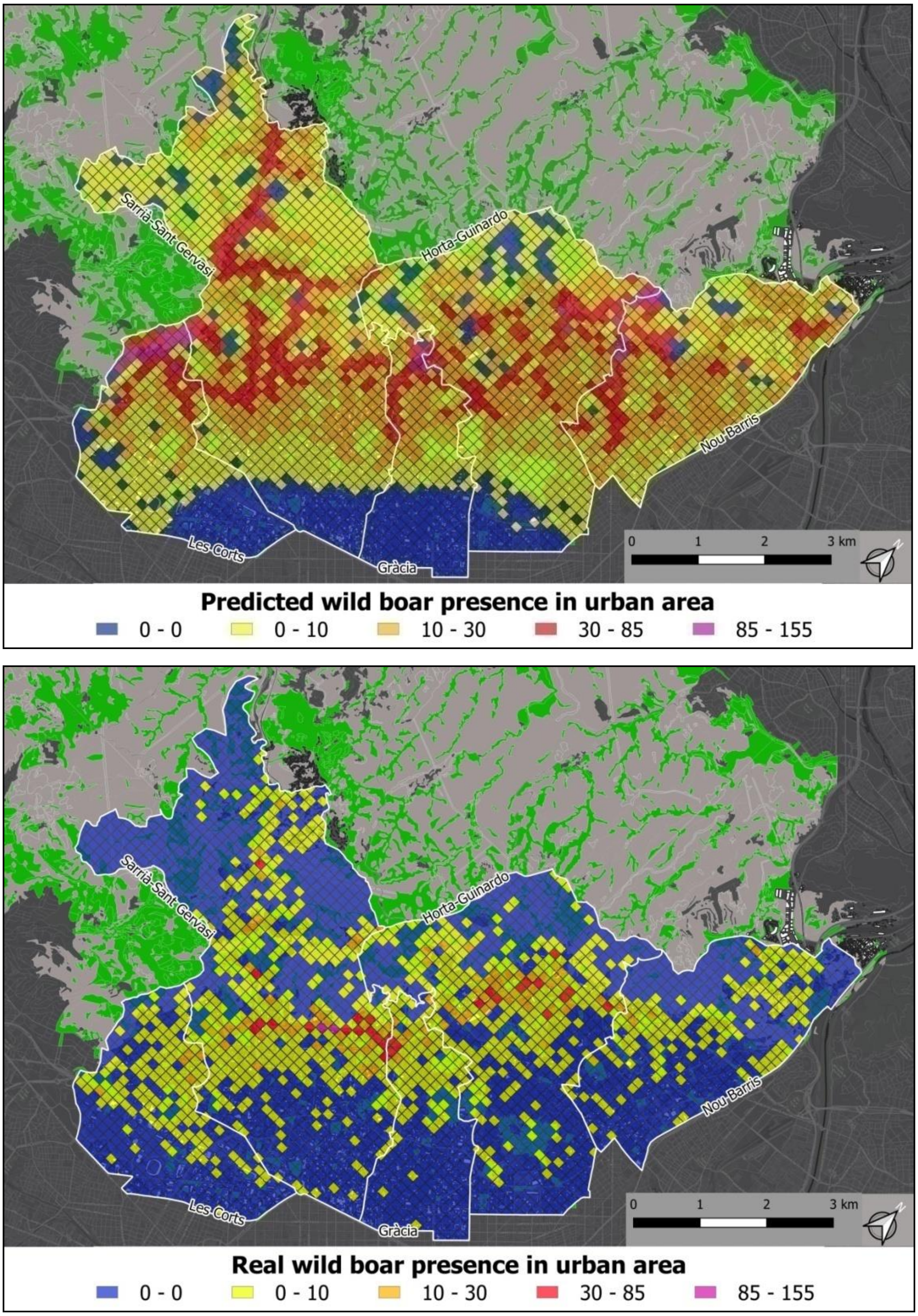


Figure 5.13. Vector maps of the WB presence in the urban area of Barcelona within the study area, as predicted by and the BCNWB model (up) and as registered by the Barcelona police department (down).

The multiple-resolution-goodness-of-fit analysis revealed an accuracy of the model to predict actual WB presences registered by the local police ranging from 0.81 (cell size=1) to 0.65 (cell size=110), with a 0.72 weighted average fit (Figure 5.13). According to the comparison of the average ratios of real and predicted WB presence, the model predicted 5.5 presences of WB for each police incidence recorded.

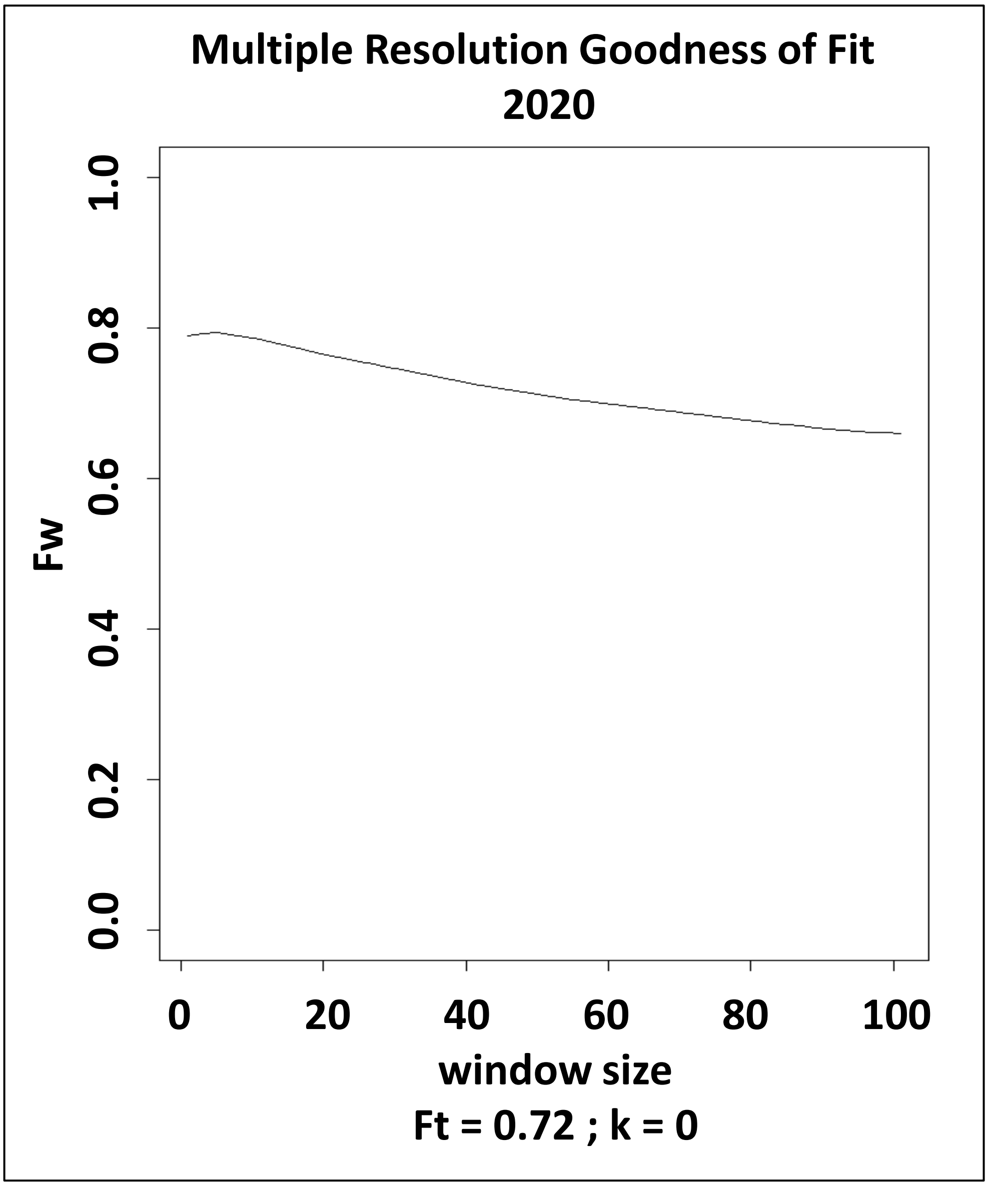
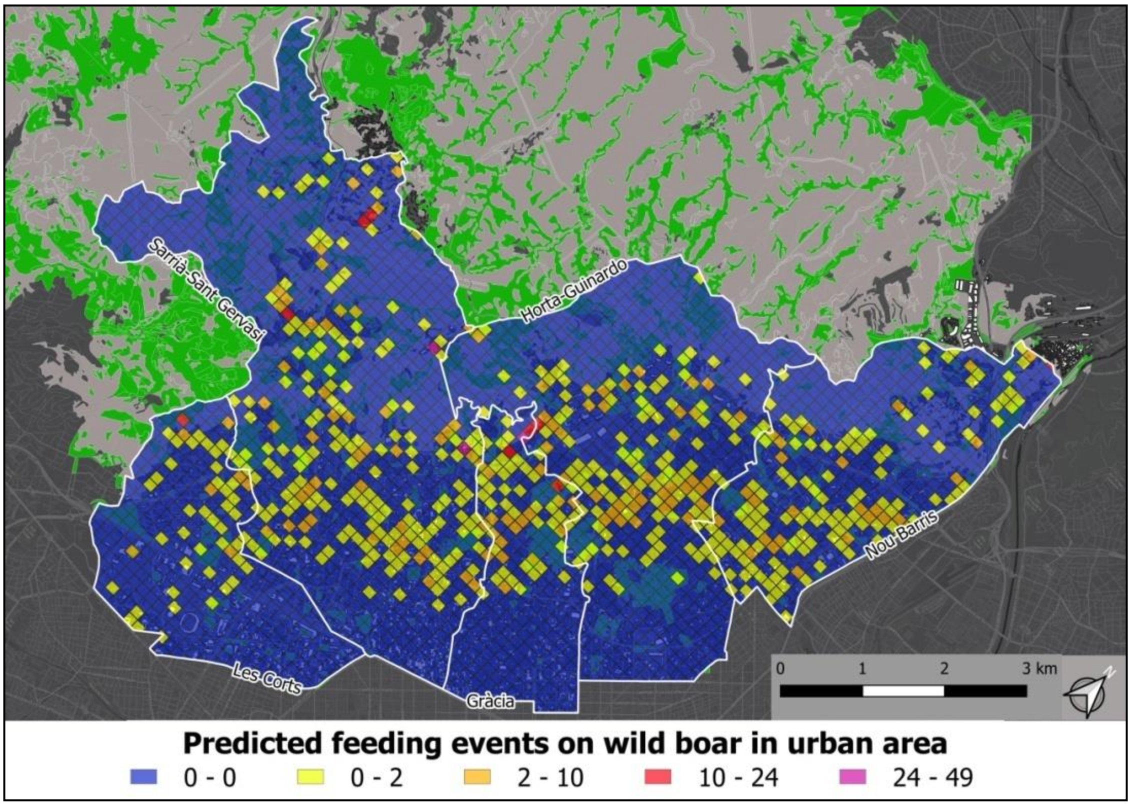


Figure 5.13. Weighted average of fits (Ft) between WB presence raster maps resulting from the model and the WB presences registered by the Barcelona police department, based on a multiple-resolution-goodness-of-fit analysis for window sizes ranging from one to 110.

Furthermore, the model predicted 115 Swb attack events on citizen agents, and 1442 direct feeding events from 1,858 citizen feeder agents offering anthropogenic food resources to Swb agents (Figure 5.15). The human-WB interactions predicted by the model showed agreement with the data collected by the authors though surveys (see Input data section c.2). The results from citizen surveys evinced an average of 150 WB aggressions every year, and a 3.24% of citizens are WB feeders when meeting Swb in the urban area, 78.26% of them occasionally.



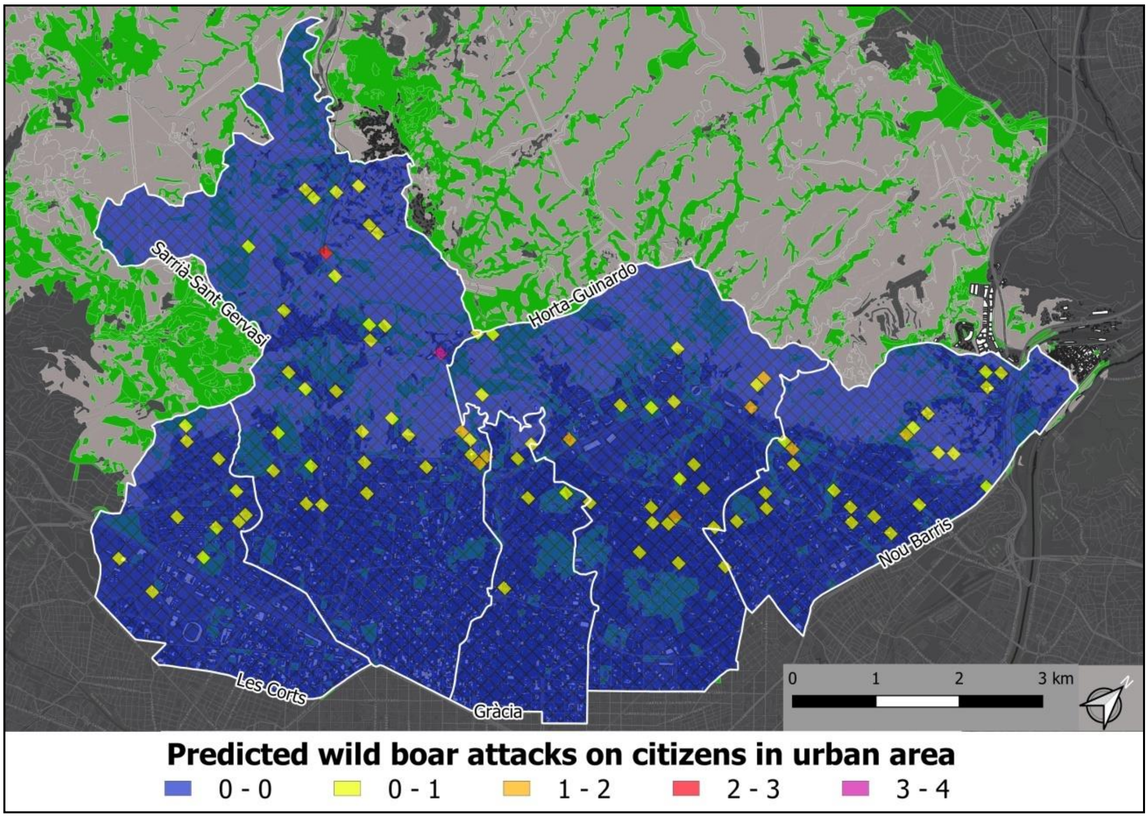


Figure 5.15. Human-WB interaction pattern maps in the urban area of BCN obtained by the BCNWB prototype. Up, feeding events (FD); down, attack events (AT).

5.2.5. Discussion

This study demonstrates the suitability of agent-based models for developing predictive models able to integrate complex social and ecological (environmental and biological) factors over time and space. Certainly, platforms such as GAMA software provide a perfect framework to develop such models and facilitate their implementation. The BCNWB prototype predicted accurately both the presence of wild boar in the study area within the urban area of BCN and the human-WB interactions. Moreover, it served as a research tool for testing the relationships between an animal population and environmental variables in space and time. The model is easy to interpret and is based on stochastic empirical data. The GIS capabilities provide the inclusion of a specific urban morphology into the model. There is a need for bottom-up explanations and account of fine-scale information in models to address pragmatic issues in ecology, such as the emergence of spatial patterns (DeAngelis & Yurek, 2017; McLane et al., 2011). The incorporation of spatial explicit models have the benefit of including scales of resolution of mechanisms able to simulate the emergence of patterns from small-scale processes, fundamental drivers of ecosystems (DeAngelis & Yurek, 2017; McLane et al., 2011).

The higher value of WB presences predicted by the model as compared to those registered by the BCN police department (3.5:1 ratio) could be related to the detectability and report ratio of a WB in the urban area. For a WB presence to be recorded by the local police, a human-WB interaction must occur and a citizen has to report it to the police. Therefore, the actual presence of WB in the study area within the urban area of BCN could be closer to the values provided by the model, the values recorded by the local police being a good proxy provided human activity and citizen habituation to WB presence in the urban area do not change significantly (Conejero et al., 2019).

The spatial concordance of the BCNWB prototype with the real presences of WB in the urban area of BCN, highlighted the relevance of anthropogenic food resources located in the urban ecosystem on the attraction and infiltration of WB into the urban area, as previously suggested (Castillo-Contreras et al., 2018). Since the model prioritized Swb movements towards feeding from anthropogenic resources located within the urban area, the high predictive correspondence suggests that the foraging behavior of the synurbic individuals of the CNP WB population was biased towards obtaining anthropogenic resources when available.

This preference for anthropogenic food resources agrees with previously published studies, either in the same population (Cahill et al., 2012a; Castillo-Contreras, 2019; Castillo-Contreras et al., 2018) or in other urban contexts, such as in Haifa, Israel (Toger et al., 2018), highlighting their major role as drivers of the WB infiltration in urban areas. However, other urban WB populations have a different behavior when foraging, prioritizing natural resources when available, such as in Berlin, Germany (Stillfried, Gras, Busch, et al., 2017). The differences suggest that prioritization of anthropogenic versus natural food resources may be determined by the early learning through experiences by interaction with the caregiver (mother) during the sensitive period in the development of juvenile WB (Worthman et al., 2010). If the scarcity period takes place before the first six months of life, which corresponds to summer in warmer regions with Mediterranean climate, juvenile WB learn to select anthropogenic food resources, as they are available throughout the year. Conversely, if the scarcity period takes place after the six months of life, namely winter in regions with colder continental climate, the juvenile WB learn to prioritize the selection of natural food resources, exploiting anthropogenic resources as a supplement when the access to natural resources is limited.

That would explain a higher synurbization rate and closer interaction with citizens of urban wild boars in Mediterranean than in Central European cities. Nevertheless, under both strategies urban WB are attracted into urban areas by anthropogenic food resources, but conventional urban wildlife management strategies usually underestimate their role and ignore their spatial distribution, hence not successfully achieving the management goals, either to promote or to control an urban population.

The model incorporates several assumptions (see Basic principles 2.2.2.1) such as WB agents do not have a preference of the type of food in a WIA, neither return to a WIA already visited in the same day. The model assumes that accordingly with the type of resources contained, some WIAs have greater MaxFood than others. Other assumption is that Police incidences are a reliable proxy of WB presence in urban area. Which in order to provide the agents

The model has also limitations such as a lack of data regarding schedule and location of feeding events, location of WIAs in urban areas and WB presence in non-urban areas from police incidences. Also, in urban areas with daily presence of WB there is a habituation of the citizens and so, a decrease of incidences registered by the police (Conejero et al., 2019). The decrease in police incidences and the lack of data in non-urban areas results in an underestimation of the magnitude of the presence of WB. In addition, due to computational limitations and in order to make the model computationally feasible, the human population was scaled by 10% to 57,347 citizen agents. The 10% of the population modeled matches the reported percentage of BCN citizens using the public area in a given hour during the foraging period of the WB (8 PM to 8 AM) (Autoritat del Transport Metropolità, 2020).

However, and despite the limitations aforementioned, the model has a high performance and is useful for the objectives of the study. The prototype model will be updated in the future as better data and technology become available. Further development of the model will include an update in the WB and citizen agents implementing a decision-based architecture to rule the behavior. The performance of the model and adjustment to the actual proxy for wild boar presence in the urban area of BCN validates the prototype, and therefore, the predictive power of the prototype can be utilized in other model designs. The prototype model can be extended with other sub-models in order to detect priority areas of human-wild boar interactions and conflicts. The location of these areas may be useful as a scientific assessment tool, through the management sub-model expansion, to apply, predict and evaluate the effect of management measures aimed to reduce the habituation process and, as a result, the WB presence in the urban area of the city. Additionally, the epidemiological sub-model expansion could act to predict and evaluate the spread and the transmission risk of pathogens, both within the WB population and in the human-WB interface, evaluating the implications for both animal and public health.

5.2.6. Conclusions

Overall, the BCNWB prototype obtained an accurate prediction of WB presence in urban area and the associated human-WB conflicts, clearly indicating and identifying the influence of anthropogenic food resources in the attraction and habituation of WB to urban areas.

The BCNWB prototype model is designed to be incremental and therefore should be considered as a first step in the employment of a combination of results from various disciplines and methodologies in the study of the management of wildlife in the urban ecosystem. The development and implementation of ABM models can provide a useful decision support tool that can be easily adapted to other animal species and other regions to cover a range of research questions and evaluate interactions, conflicts and disease transmission potential at the wild-domestic-human interface.

5.3. Study 3

Assessing the animal and public health hazard of urban wild boars using an Agent-Based Model approach.

5.3.1. Abstract

Wild boar (WB, *Sus scrofa*), which population densities are increasing globally thanks to its great adaptability and plastic behavior, plays a major epidemiological role as pathogen host. The increase in WB urban populations is associated to new close human-WB interactions, which generate an increasing concern regarding the epidemiological risk for public health. Synurbization favored by the availability of anthropogenic food resources, increases aggregation and conspecific tolerance, enhancing the contact rates of synurbic wild boar and citizens, with the consequent risk of pathogen transmission.

This study is an epidemiological expansion of the BCNWB-prototype, a validated agent-based model of the ecological and social factors driving the use of the urban ecosystem by synurbic WB and the related human-WB interactions in Barcelona, Spain (Study 2). The BCNWB-EPI model aims to test different epidemiological scenarios that could inform health risk assessments and support risk-based decision-making. Here we focus on the epidemiological dynamics at (peri)urban scale of three relevant pathogens at risk of transmission at the wild-domestic-human interface: hepatitis E virus (HEV), antimicrobial resistant *Campylobacter* (AR-CB) and African swine fever virus (ASFV).

In the ASFV scenario, the entire WB population was exposed to the virus 51 to 71 days after the index case (first case in the population). ASFV transmission was mediated by carcasses in 87.6% of the cases and by direct contact in the remaining 12.6%. The outbreak lasted between 71 and 124 days, reducing 95% of the initial population, similar to previous reports of ASFV outbreaks in other European countries. Model outputs of citizen exposition for HEV and AR-CB (according to the model, 457and 462 humans would have contacted the pathogen, respectively) were in agreement with the World Health Organization (WHO) estimations (480 for HEV and 264 to 558 for AR-CB) for the modelled human population in the estimated time extent. Despite the difference in the prevalence of pathogens (20% and 60% for HEV and AR-CB, respectively) hosted by the WB population, the similar number of exposed citizens in each pathogen scenario suggest the major role of feces in the transmission of these pathogens, resulting consequently in anon-negligible risk for public health. The epidemiological prediction generated by the model can be used to inform risk assessments to evaluate the animal and public health risks posed by the spread of these pathogens within the wild boar and between the wild boar (acting as environmental sources) and the Barcelona inhabitants.

Keywords

African swine fever virus, agent-based model, *Campylobacter*, hepatitis E virus, urban wild boar

5.3.2. Introduction

The emergence in 2019 of the novel severe acute respiratory syndrome–coronavirus 2 (SARS-CoV-2), has boosted the increasing concern and associated implications of zoonotic pathogens at the wildlife-human interface. Zoonoses are defined as any disease or infection transmissible from vertebrate animals to humans and caused by different agents such as viruses, bacteria, fungi, parasites or other unconventional agents (i.e. prions) (World Health Organization, 2020c), and represent 61% of human diseases (Cunningham, 2005) and 75% of emerging infectious diseases, which are mainly originated from wildlife (Blancou et al., 2005). The onset of outbreaks and epidemics of previously unknown human infectious diseases emerging from animal reservoirs (i.e. Ebola virus, West Nile virus, SARS and highly pathogenic avian influenza viruses (HPAI)) has evidenced the significant risk posed by biological agents for public health and animal breeding activities (Rabozzi et al., 2012). However, the risk of zoonoses and associated implications, particularly in occupational settings (Rabozzi et al., 2012), has historically been highly underestimated. The cases of HPAI and most recently SARS-CoV-2 have evidenced that emerging diseases may rapidly spread and become endemic, causing a major public health concern requiring lockdown of entire countries, with the consequent severe impact not only on public health but also on the economy of whole regions.

Eurasian wild boar (WB) (*Sus scrofa*) and other wild pigs are considered not only a public health risk but also for swine production and game industry (Castillo, 2019; Ruiz-Fons, 2017). The emergent concern is based on the increase in distribution and abundance, resulting from a plasticity behavior and great adaptability to different landscapes (Castillo-Contreras et al., 2018; Massei et al., 2011; Morelle et al., 2015) and a major epidemiological role as pathogen host (Fernández et al., 2006; Meng et al., 2009; Ruiz-Fons, 2017). As a result, within the synurbization process (Luniak, 2004), WB is colonizing urban areas (Cahill et al., 2012a; Castillo-Contreras et al., 2018; Stillfried et al., 2016; Toger et al., 2018), process originated by a higher tolerance to human disturbance (Stillfried, Gras, Börner, et al., 2017) and the availability of anthropogenic food resources (Cahill et al., 2012a; Castillo-Contreras et al., 2018; Llimona et al., 2007).

WB plays a major epidemiological role as host for zoonotic and non-zoonotic pathogens (Fernández et al., 2006; Hassell et al., 2017; Ruiz-Fons, 2017) shared with livestock, companion animals and humans, participating in the maintenance of multi-host pathogens (Fernández-Aguilar et al., 2018; Haydon et al., 2002; Meng et al., 2009; Wang et al., 2019). The epidemiological role of WB gains relevance in urban areas, where anthropogenic resources foraged by synurbic WB may amplify pathogen spread by increasing host aggregation and tolerance (Becker et al., 2015, 2018; Tucker et al., 2020). Human activities may be the source, influencing the carriage and potential spread of antimicrobial resistant bacteria on wild boar (Castillo-Contreras, 2019; Navarro-Gonzalez et al., 2018; Swift et al., 2019; Vittecoq et al., 2016). Under these circumstances, changes in host contact rates and immunity can produce strong non-linear responses in pathogen invasion and prevalence (Becker et al., 2015).

Following the One Health approach, the dynamics of a zoonotic agent in a multi-host pathogen system involve transmission among host species (including humans), where contact is a key feature of both reservoir and disease emergence dynamics and of the recovery or mortality rate of infected individuals (Hassell et al., 2017; Viana et al., 2014). The risk of human spillover is determined by the prevalence of infection in the host population, the rate of contact between humans and infected individuals, and the probability that infection occurs upon contact (Begon et al., 2002; Davis et al., 2005; Hassell et al., 2017; Lloyd-smith et al., 2009).

The new relationship status between synurbic WB and urban citizens in densely populated areas, has modified the social-ecological system involved in human-wild boar interactions (Conejero et al., 2019; Lischka et al., 2018; Luniak, 2004). The increased aggregation produced by anthropogenic resources in urban areas enhances the contact rates of synurbic WB and citizens (Becker et al., 2015, 2018; Castillo-Contreras et al., 2018; Toger et al., 2018), the risk of exposure to pathogens and therefore, the concern about the role of WB as potential source for emerging human diseases (Blancou et al., 2005; Hassell et al., 2017; Meng et al., 2009; Ruiz-Fons, 2017). Interactions can be direct, such as citizen direct feeding to WB, touching or petting WB and weak bites produced while demanding food, or indirect, such as contact with feces and urine in green areas and playgrounds. Transmission may therefore occur by oral, respiratory, conjunctival and transdermal routes as well as through skin wounds (Ruiz-Fons, 2017).

In such conditions of close contact between WB and human populations, the pathways of pathogen transmission are driven by the interactions within and between species and consequently, estimating the contact rate is crucial to identify the potential transmission pathways. In WB, contact rates are strongly constrained socially. Young WB (<2 years) show exceptional connectivity among-group within the population, and the most frequent associations occur at distances of 0–1 km (mostly within groups), less frequent at 1–3 km (mostly between groups), and sporadic at >4 km (Podgórski et al., 2018).

The Barcelona Metropolitan Area (BMA) is one of the largest European metropolitan areas, with 3.2 million people and 636 km^2(population density of 5,000 people per km2) (Àrea Metropolitana de Barcelona, 2020)The 80 km^2 Natura 2000 Collserola Natural Park (CNP), located within the BMA, hosts a WB population which is partially habituated to humans (Cahill et al., 2012a; Castillo-Contreras, 2019; Castillo-Contreras et al., 2018; Conejero et al., 2019), Study 1). Synurbic WB from the CNP raid in the (peri)urban area of the city attracted by anthropogenic resources (Cahill et al., 2012a; Castillo-Contreras et al., 2018; Conejero et al., 2019). While foraging in the urban area, the synurbic WB contact with green areas and street furniture, health and school facilities and citizens involving all age and health state combination. Although the CNP is virtually isolated from the nearby natural and agricultural areas by urban development and road and train networks (Cahill & Llimona, 2004), WB use some riparian areas and dry riverbeds as corridors and ecological connectors, hence allowing some movements out of this area (Castillo-Contreras et al., 2018; Sánchez-Montoya et al., 2016).

Previous studies on the BMA WB population have detected zoonotic hepatitis E virus (Wang et al., 2019), *Streptococcus suis* (Fernández-Aguilar et al., 2018), tick-borne pathogens such as *Rickettsia* spp. (Castillo-Contreras, 2019), and antibiotic resistant bacteria (Castillo-Contreras, 2019; Navarro-Gonzalez et al., 2018).

Hepatitis E virus (HEV) is a single-stranded, positive-sense RNA virus, classified in the family *Hepeviridae* (Pavio et al., 2015). The strains infecting mammals are classified in the genus *Orthohepevirus,* with five genotypes infecting humans, each one divided into 1–11 subtypes (Wang et al., 2019). The genotypes HEV3 and HEV4 are zoonotic viruses shared with pigs worldwide, thus, wild boar may constitute true reservoir host for HEV (Kukielka et al., 2016; Ruiz-Fons, 2017). HEV is commonly transmitted via the fecal–oral route (Wang et al., 2019) and outbreaks have been linked to WB meat consumption (Rivero-Juarez et al., 2017). HEV infections are generally self-limiting with low mortality. HEV3-infected immune compromised individuals are at risk of developing chronic infections associated with rapid progression of liver disease and cirrhosis (Kumar et al., 2013; Pas et al., 2012). The BMA wild boar population has a 20% prevalence (20%) of HEV infections (HEV3 genotype, subtypes 3fand3c/i), indicating that zoonotic transmission from wild boar may be more common than previously anticipated (Wang et al., 2019).

Campylobacter spp. and *Escherichia* spp. (Castillo-Contreras, 2019), are also both a public health concern. Campylobacteriosis is considered the most common bacterial cause of human gastroenteritis worldwide (World Health Organization 2020a). WB constitutes a reservoir of *Campylobacter* species, including antimicrobial resistant and multi-resistant strains (Carbonero et al., 2014; Castillo-Contreras, 2019). Although *Campylobacter* commonly cause self-limiting disease, they can also produce fever, abdominal pain, diarrhea, reactive arthritis, Guillain-Barré syndrome and chronic colitis, and up to 10% of the cases may require medical intervention (Moore et al., 2005). The risk can increase with decreased immune systems, such as in elder people or people with impaired immunity (Moore et al., 2005). The main route of transmission is generally believed to be food borne, via undercooked products, contaminated milk, water and ice (including contact with contaminated water during recreational activities). In animals, *Campylobacter* seldom causes disease, but as a zoonosis, it can be transmitted to humans from animals or animal products, most often from feces (World Health Organization 2020a). *Campylobacter* have been frequently isolated from asymptomatic companion animals, with symptoms of enteritis frequently reported in younger animals ,and transmission from pets to humans has been confirmed and identified as a potential risk factor in epidemiological investigations, particularly young children in contact with puppies exhibiting enteric symptoms (Moore et al., 2005). Most (60.8%) WB in the BMA carried *Campylobacter* spp. Thirty-five per cent of the isolates had high virulence genes and all the *Campylobacter* isolates tested were resistant to at least oneantimicrobial,68.2% of them multi-resistant (Castillo-Contreras, 2019).

AFSV, an OIE (World Organization for Animal Health) List A virus, is a DNA virus in the family *Asfarviridae* (Meng et al., 2009). ASFV is highly contagious, affecting domestic pigs and WB with fever, hemorrhages and resulting in up to 100% morbidity and mortality in previously unexposed WB with no treatment or vaccine (Costard et al., 2013; EFSA, 2014). It is transmitted through direct contact, ingestion of contaminated feedstuffs and ticks (More et al., 2018). The current European wild boar density appears to facilitate the onset of ASFV and the role of the species as reservoir for this virus (More et al., 2018).

Although no case of African swine fever (ASFV) has been reported in Spain since the eradication from the Iberian Peninsula in the late 1990s (Arias & Sánchez-Vizcaíno, 2008), the recent emergence and spread of ASFV in several Eastern and Central

European countries (Arias et al 2013) are linked to the movement of both wild boar and anthropogenic resources (De la Torre et al., 2015; Guinat et al., 2016). The pork industry is a major economic sector in Catalonia (Spanish administrative region where the BMA is located), with 5,930 pig farms and 9,414,802 pigs in 2019 (Departament d'Agricultura, Ramaderia, Pesca i Alimentació, Generalitat de Catalunya, 2019a)., accounting for 2.646 million Euros in exports in 2019 (PRODECA and Departament d'Agricultura, Ramaderia, Pesca i Alimentació, Generalitat de Catalunya, 2020). ASFV is a major concern for national and regional governments because the devastating economic impact for the pork industry associated to high morbidity and mortality and trade restrictions (Castillo, 2019; Gavier-Widén et al., 2015; Sánchez-Cordón et al., 2018). Due to the human origin of ASFV outbreaks, particularly of those distant from the distribution area of the disease, the growing human-wild boar interface at the BMA is a potential origin for an ASFV outbreak in the region.

Even though all the evidence warning about emerging and reemerging diseases remains as a major concern to both national and regional economy and public health, there is a general need for an early warning system predicting the risk of an epidemic or detecting early signs of onset (Rabozzi et al., 2012). A better understanding of the wildlife–pathogen dynamics in the human-wildlife interface is needed to produce accurate health risk assessments supporting policy makers in the implementation of the best mitigation strategy. A useful decision-making tool should evaluate a mitigation strategy as a combination of the most efficient and effective interventions, aimed to reduce and prevent the public health risks posed by disease emergence.

To better understand the factors and mechanisms that may influence the propagation of these pathogens, field or *in-vitro* studies results are not completely satisfactory. Thus, theoretical (virtual) epidemiology considers simulated models of reality to test hypotheses concerning the environment, the social structure and the behavior of the animals, among other factors (Amouroux et al., 2008).The most important requirements for theoretical epidemiology virtual scenarios to address epidemiological challenges are (1) Extensively representation of the environment together with its own dynamics; (2) Framework at both population level and individuals; (3) Interactions at the population or individual levels, and with the environment; (4) Data able to be reused in the modeling of the system;(5) An able simulation platform to run virtual scenarios (Amouroux et al., 2008).

There is a need for spatial models that account for surveillance strategies sufficiently flexible to adapt to the circumstances of a disease emergence (Burroughs et al., 2002) and for the effects of anthropogenic resources on local dynamics and movement connectivity to understand the persistence and spatial spread of pathogens (Becker et al., 2015, 2018). Several types of epidemiological models have been proposed (Amouroux, 2011). However, only the joint use of spatially explicit Agent-Based Modeling (ABM) together with GIS approach, can fully represent heterogeneous agents coupled with a detailed and flexible representation of the environment (Amouroux et al., 2008) to better evaluate diverse eco-epidemiological scenarios. Therefore, according to the data available to meet the theoretical epidemiology requirements and both relevance and implications to public health and national and regional economy, (1) antibiotic resistant *Campylobacter* (AR-CB), (2) HEV and (3) ASFV have been selected for the present study.

The objective of this study is to expand a previously developed ABM of contacts at the human-WB interface (BCNWB model) to include an epidemiological sub-model, the BCNWB-EPI model. This BCNWB-EPI model will allow testing different epidemiological scenarios and producing valuable risk assessment estimates to support decision-making. The main aims are to: (1) identify high risk areas to inform risk-mitigation strategies to reduce the exposure of the BCN citizens to zoonotic pathogens (HEV and AR-CB) and (2) evaluate the associated ASFV potential risk of contact and evolution of the resulting outbreak, transmitted by contaminated anthropogenic resources, as a potential entry point of ASFV in the Spanish WB population.

5.3.3. Material and Methods

5.3.3.1. Study area

As described in the BCNWB prototype model (Study 2), the synurbic wild boars forage essentially in the five districts of the city bordering with CNP, with sporadic incursions in the inner part of the city (Castillo-Contreras et al., 2018). The study area includes therefore the five more affected districts (Les Corts (LCOR), surface 6.02 km^2 and population 81,974 inhabitants; Sarrià-Sant Gervasi (SSGE), surface 19.91 km^2 and population 149,260 inhabitants; Gràcia (GRA), surface 4.19 km^2 and population 121,798 inhabitants; Horta-Guinardó (HOGI), surface 11.96 km^2 and population 171,495 inhabitants; and Nou Barris (NOBA), surface 8.05 km^2 and population 170,669 inhabitants) (Figure 5.16; Ajuntament de Barcelona, 2020). Health centers are located within the limits of the five districts, including the biggest hospital in Barcelona. In the immediate surroundings of the hospital facilities, the synurbic WB roam in search of food, offered by patients and visitors, creating a chance for disease transmission in this new human-WB interface.

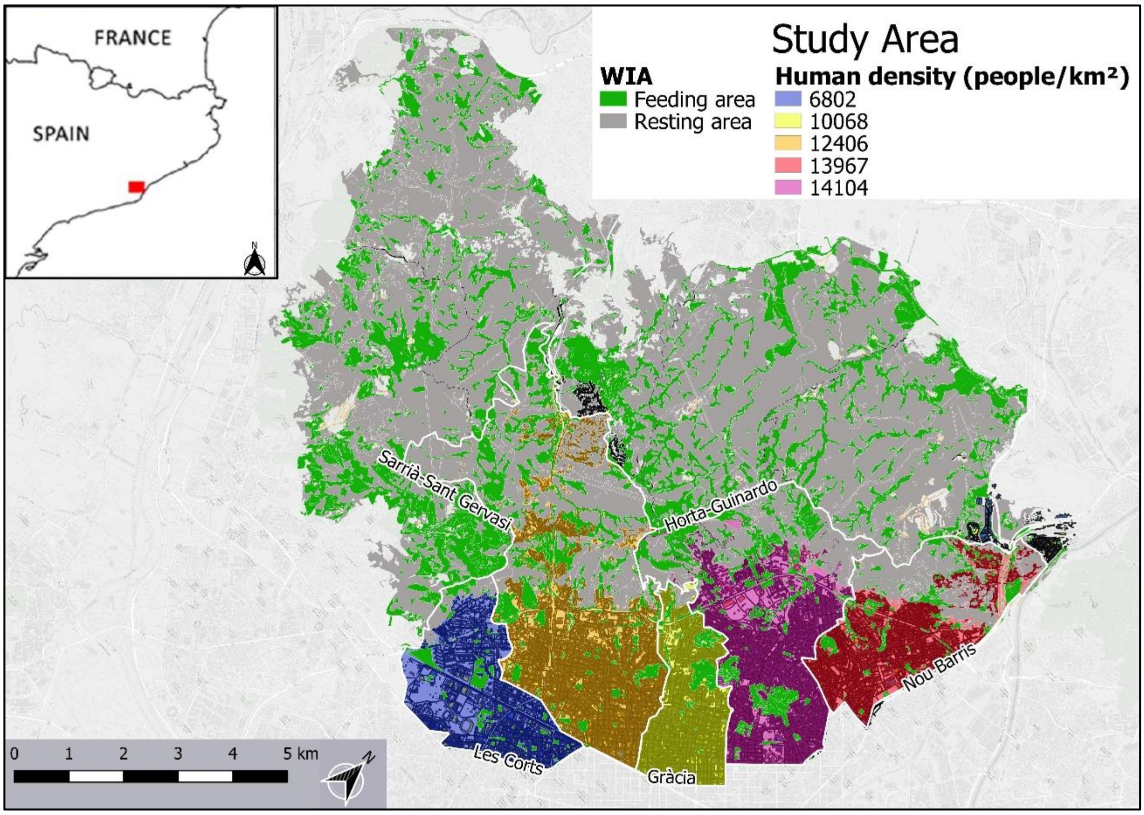


Figure 5.16. Study Area. Collserola Natural Park and the five districts of Barcelona (LCOR, Les Corts; SSGE, Sarrià-Sant Gervasi; GRA, Gràcia; HOGI, Horta-Guinardó; and NOBA, Nou Barris), included in the model. Population density and wild boar interaction areas (WIA, feeding and resting areas).

5.3.3.2. Model Description

The present study is an epidemiological expansion of the BCNWB prototype, a verified, calibrated and validated simulation from an ABM approach of the synurbization process of the CNP WB in the BMA, the use of the urban ecosystem of Barcelona city by synurbic WB and human-WB interactions, considering environmental, biological and social factors (Figure 5.17, Study 2). The present study addresses the description of the Epi module. The model follows the standard O.D.D. (Overview, Design concepts, Details) protocol (Grimm et al. 2010). The model was implemented in GAML language using GAMA platform, an open-source and AMB multi-platform combined with GIS capabilities (Taillandier et al., 2019).

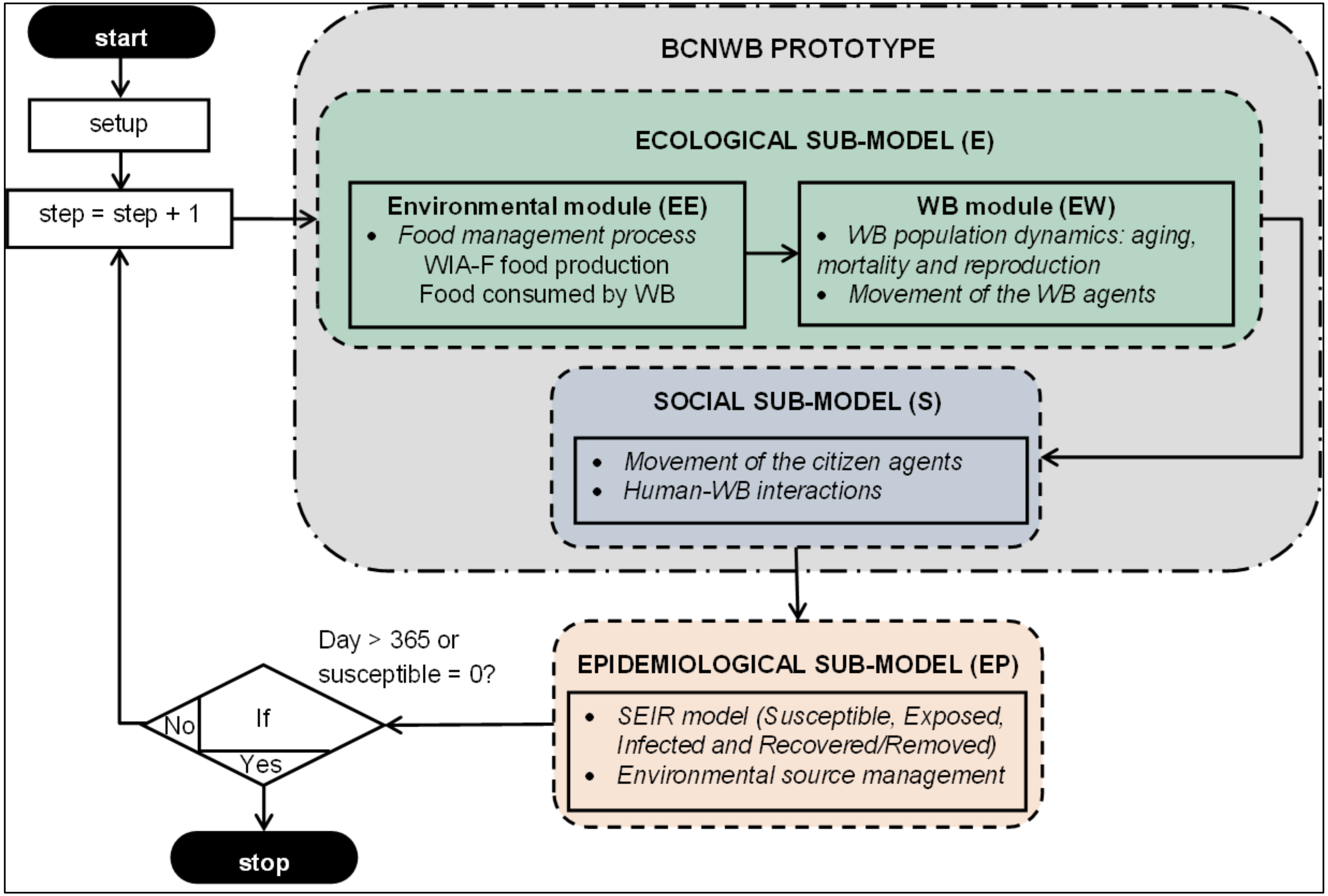


Figure 5.17. Flow chart diagram of the BCNWB-EPI model. Including the BCNWB prototype (with the Ecological sub-model containing both environmental and WB modules and the social sub-model) and the epidemiological sub-model.

a) Overview

a.1) Purpose

The purpose of this study is to develop the BCNWB-EPI model, an epidemiological expansion (Figure 4.2) to the BCNWB model (Study 2), which includes an epidemiological sub-model (EP) using an ABM approach (see sub-model section c.3). The final objective is to produce estimates for health risk assessment of specific pathogens by evaluating disease direct or indirect transmission within the WB population and between WB and humans in BMA, Spain. The aim in this BCNWB-EPI model is focused in simulating and understanding how the social-ecological system (Lischtka 2018) of the human-WB interactions in the urban area of Barcelona, influences the epidemiological processes of disease transmission within the WB population and at the human-WB interface. The three pathogens selected to illustrate our model are major concerns both for animal and public health and to national and regional economy. HEV and AR-CB are both zoonotic pathogens present in the CNP WB population (Castillo-Contreras, 2019; Navarro-Gonzalez et al., 2018; Wang et al., 2019). ASFV is a disease of swine that is currently expanding in Europe and Spain, as any other European country, is at high risk of ASFV anthropic re-introduction, which would devastate the Spanish swine industry, which is a top producer and exporter in the European Union (PRODECA and Departament d'Agricultura, Ramaderia, Pesca i Alimentació, Generalitat de Catalunya, 2020). The model initialized with the data of actual WB presence in the urban area in 2019 to generate accurate health risk assessments with the aim to support policy makers.

a.2) Entities, state variables, and scales

The study focused on the epidemiological dynamics of three pathogens at a metropolitan area scale (110 $km^2$of natural ecosystems in the CNP and 13.15 $km^2$of urban ecosystem in the city of Barcelona in addition to a 100-meter-wide fringe of the boundary between both ecosystems, managed by the Barcelona City council) during one year. Thus, the present study was divided in three epidemiological scenarios, (1) HEV scenario, (2) AR-CB scenario and (3) ASFV scenario. To get enough accuracy and quality output data in the model, each step represented one hour of the day.

The model included a grid agent (100x100 meters) covering all the study area to store the spatially-explicit results and the five main agents included in the BCNWB model (Study 2), namely: (1) WB interaction areas (WIA) classified into WIA-F (feeding areas) and WIA-R (resting areas); (2) buildings classified into business (office or factory), residential (houses), leisure (shopping or sport) and health facilities (hospitals); (3) the

BMA road network, containing the road, path and hydrographic networks; and the susceptible mobile agents (4) CNP WB containing sex and age classes subtypes (male and female and juvenile, yearling and adult); and (5) Barcelona citizens classified into regular citizens, pet owners and WB feeders. Furthermore, the epidemiological sub-model included a new agent involved in the pathogen transmissions, (6) the environmental sources (ES), representing WB feces in the HEV and AR-CB scenarios and WB carcasses in the ASFV scenario, as those are considered to play a major role in transmission of each pathogen (Campagnolo et al., 2018; Khomenko et al., 2013; Kumar et al., 2013; Lange & Thulke, 2017)

- **State variables**

Besides the state variables included in the BCNWB model, the epidemiological sub-model incorporated variables specific for the different agents involved in the pathogen transmission (Table 5.7 and 5.8). According with the reference values of each pathogen, the values of the epidemiological state variables varied depending on the scenario.

Table 5.7. State variables included by the epidemiological sub-model for the susceptible mobile agents and values for each scenario (HEV, Hepatitis E virus; AR-CB, Antimicrobial resistant *Campylobacter*; and ASFV, African Swine Fever Virus).

Variable (description)	Type	Agent	Value (initial value)	Reference
Is_Susceptible (condition of the host/mobile? agent to be vulnerable to transmission events of the pathogen)	Bool	Wb	True-False (HEV=80%, AR-CB =40%, ASFV=100%)	HEV, (Wang et al., 2019); AR-CB, (Castillo-Contreras, 2019); ASFV, ((EFSA, 2014))
		Citizen	True-False (100%)	
Is_Exposed (condition of the WB agents during the incubation period, infected, but not yet infectious)	Bool	Wb	True-False (0%)	
		Citizen	True-False (0%)	
Is_Infected (condition of the agent infecting and expressing the disease)	Bool	Wb	True-False (HEV=20%, AR-CB =60%, ASFV=0%)	HEV, (Wang et al., 2019); AR-CB, (Castillo-Contreras, 2019)

Is_Resistant (condition of the agent to be infected but neither expressing or infecting anymore)	Bool	Wb	True-False (ASFV=0 %)	
Is_atRisk (condition of the citizen agents to be more susceptible to the pathogen due to health or age factors)	Bool	Citizen	True-False (HEV, AR-CB= 20%)	
Transmission_dist (distance between agents where a transmission event can take place)	Float	Wb	ASFV=5 m	
Proba_infection (probability in each step of a transmission event between agents, when an agent contacts other agent and becomes exposed)	Float	Wb	ASFV=0.99	(EFSA, 2014)
Proba_recover (probability of an agent to recover from infection and develop resistance to the pathogen)	Float	Wb	ASFV=0.05 0.95 mortality	(Perez et al., 1998)
Incubation_period (time from exposition to onset of clinical signs or latency period)	Float	Wb	ASFV= 4 days post infection	
Infection_period (time from onset of infectiousness to death or recovery)	Float	Wb	ASFV=5-11 days post infection	(EFSA, 2014)
Proba_die (probability of an agent to die from infection)	Float	Wb	ASFV=0.99/7 days	

Table 5.8. State variables included by the epidemiological sub-model for the environmental source agents and values for each scenario (1, AR-CB; 2, HEV; and 3, ASFV).

Variable (description)	Type	Agent	Value	Reference
Proba_infection (probability in each step of a transmission event when a susceptible mobile agent is inside the transmission distance and becomes exposed)	Float	ES	HEV =0.01375	0.66 daily in pigs (Bouwknegt et al., 2009)
			AR-CB =0.0108	0.13 daily in broilers (Neves et al., 2019)
			ASFV=0.99	(EFSA, 2014)
Viability_time (survival of the pathogen in the environment)	Float	ES	HEV =45 days	(Cook & van der Poel, 2015)
			AR-CB =5 days	(Whiley et al., 2013)
			ASFV=56 days	(Guinat et al., 2016)
Transmission_dist (distance between agents where a transmission event can take place)	Float	ES	HEV, AR-CB= 0.5 m	
			ASFV= 300 m*	

*Representing the distance where WB can detect a carcass, creating the conditions for a contact (Probst et al., 2017).

a.3) Process overview and scheduling

As described in the BCNWB model, at each step of the simulation, first the environmental sub-model was executed creating the simulated environment, and then the processes related to the WB (population dynamics (PD) and movement) and the social sub-models (citizen movement) were executed consecutively. Briefly, WB agents started the simulation in a resting state in a WIA-R, and when the foraging activity began the WB agent moved between WIA-F, starting from the closest to the initial location, moving back when it was time to rest to the closest WIA-R. Each citizen agent had an assigned residential and business building throughout the simulation extend. During labor days (Monday to Friday), the activity of the citizen agents started from a residential building, moving to a business building and returning at the end of the workday to the residential building. During the weekend, the citizen agents changed their destination for recreational activities in leisure buildings and WIA-F (representing outdoor activities such as going to urban green areas and paths in the CNP). Then, the epidemiological sub-model was executed; for each scenario, the schedule was modified according with the parameterization of the epidemiological characteristics of the pathogen. The individual epidemiological actions could be contacting another agent, getting infected, transmitting the pathogen, recovering and die.

- **Model verification, calibration and validation**

The evaluation of the BCNWB model was applied (Study 2) by verification, calibration and validation (Heppenstall et al., 2012; Xiang et al., 2005). The verification of the epidemiological sub-model was performed independently to verify the correct behavior of the modeled epidemiological processes involved. Afterwards, the epidemiological sub-model was integrated in the BCNWB model and calibrated with the epidemiological data of the CNP WB population.

The transmission rates for each zoonotic pathogen (HEV and AR-CB) were calculated from experimental infections in other species (Table 4.2, (Bouwknegt et al., 2009; Neves et al., 2019)). Departing from the published values, intraspecific daily rates were transformed into interspecific transmission hourly rates with base 12 to adjust for an initial two-hour interval (i.e., two steps of the simulation). Then, by means of factorial sensitivity test performed on a one-month simulation the rates were compared with the estimated average monthly human exposure to each pathogen (World Health Organization 2020b and 2020a) to select the best value.

In the (1) HEV and (2) AR-CB scenarios, the validation of the model was done by comparing the number of exposed citizens at the end of the simulation with WHO reports of annual exposition of CB (World Health Organization 2020a) and HEV (World Health Organization 2020b). In the (3) ASFV scenario validation was performed by comparing with previously reported outbreaks for ASFV the basic reproduction number calculated by the model and the number of resistant WB at the end of the outbreak. The scenario was considered validated if the differences between the predicted data resulting from the model and the data used for validation were below 10%.

In order to visualize and analyze the results, vector maps were created using the software QGIS v3.2 Bonn (Quantum GIS Development Team 2018).

b) Design concepts

b.1) Basic principles

The epidemiological sub-model implemented in the ABM approach is based on a SEIR (Susceptible, Exposed, Infected and Recovered or Removed) model. The general knowledge of the natural history of the three pathogens included in the present study originated from previous studies of the population or literature review (see input data section c.2). The daily activity of the susceptible mobile agents increased the citizen-WB interactions and also contacts with environmental source agents, raising the transmission risk.

Since the scope of the present study and objectives of the model is evaluating the pathogen WB-WB or WB-human transmission risk, conditions were established in the epidemiological sub-model: (1) only WB agents could spread the pathogens; (2) the SEIR structure was only fully implemented in the ASFV scenario, as the objective is to evaluate the transmission risk and impact of the pathogen within the WB population; however, in the AR-CB and HEV scenarios, the prediction of transmission to human was more important, so in an attempt to avoid underestimations of the risk of transmission, the prevalence of the pathogen in the WB agents was constant throughout the simulation; (3)citizen agents got exposed to the pathogen only from ES (feces), but did not become infected, transmit or recover as the human epidemiological process is out of the scope of the present study; (4) the model considered those citizen agents whose immune system was compromised for health or age reasons at risk (Is_atRisk) and therefore, more likely to develop severe infections. With the aim to produce quality health risk assessments, the model stored for results the number and location of the expositions to the pathogens of all the citizen agents and those at risk independently.

b.2) Emergence

The emergence outcomes of the model were the dynamics of the pathogens circulating in the BMA WB population during the foraging activity in the urban area, and the spillover to humans, which emerged from the individual status and both direct and mediated transmissions.

b.3) Adaptation

The pathogen transmission was an adaptive process taking place all over the simulation extent only when an infected agent contacted either a susceptible mobile or environmental source agent, responding to an infection probability (proba_infection, internal factor) and a transmission distance (transmission_distance, external factor).

Also, the individual resistance of the agents to each pathogen was an adaptive process taking place over the simulation extend but only when the agent was infected and in response to a recovery probability (proba_recover).

b.4) Sensing, Interaction and Observation

Aside from the sensing and interactions in the BCNWB model, which included the sensing of the mobile agents (Wb and citizens) and WIA-F agents among them and the human-WB interactions (WB attacks and feeding events), the epidemiological sub-model extension included specific interactions for disease transmission. The epidemiological interactions were direct transmission between susceptible mobile agents (WB to WB and WB to citizen) and indirect transmissions, mediated by environmental source agents. In the model, all the interactions between the agents were direct interactions. Direct interactions referred to the contact of two agents, mediated by the spatial proximity between them, where one of those agents could infect the other agent with the pathogen, according to a possibility. The information was stored into the grid agent and used for results, validation and calibration. Indirect transmissions were modeled separately as indirect interactions, from a WB agent to an ES agent and then to a mobile agent (WB or citizen). Consequently, ES agents could sustain the pathogens according with their epidemiological characteristics (see Input data section c.2 and Sub-model section c.3.a). ES agents sense the mobile agents located within the Transmission_distance. The information is stored into a list and used to execute the epidemiological sub-model (see Sub-model section c.3.a).

b.5) Stochasticity

Stochasticity was included in the BCNWB prototype as an environmental variation (ranging randomly +-15%), influencing the PD of the WB population (mortality and fertility rates) and Food production in WIA-F.

b.6) Collectives

The epidemiological sub-model included the collectives of the SEIR model for WB and citizen agents, namely susceptible, exposed, infected and recovered. The differences between them were the aptitude to transmit the pathogen and an increased mortality in the ASFV scenario.

c) Details

c.1) Initialization

The BCNWB-EPI model started from the historical time set at January 1st 2020. In the beginning of the simulation (Figure 5.18), the non-infected synurbic WB (Swb) agents were located according to the WB GPS locations provided by the BCN local police in 2019.The initial locations of infected WB and non-infected non-urban WB (Wwb) agents were based on the GPS location where the WB was hunted or captured. The citizen agents were located in random residential buildings, according to the number and proportion in each district and citizen sub-type registered by public available data and data gathered by the authors (see input data section c.2). The total population considered for the model excluded citizens below three and above 85 years due to the lack of mobility. As a result of computational limitations, the model started with 10% of the human population, thus a population of 57,329 citizen agents randomly initialized inside a resting building.

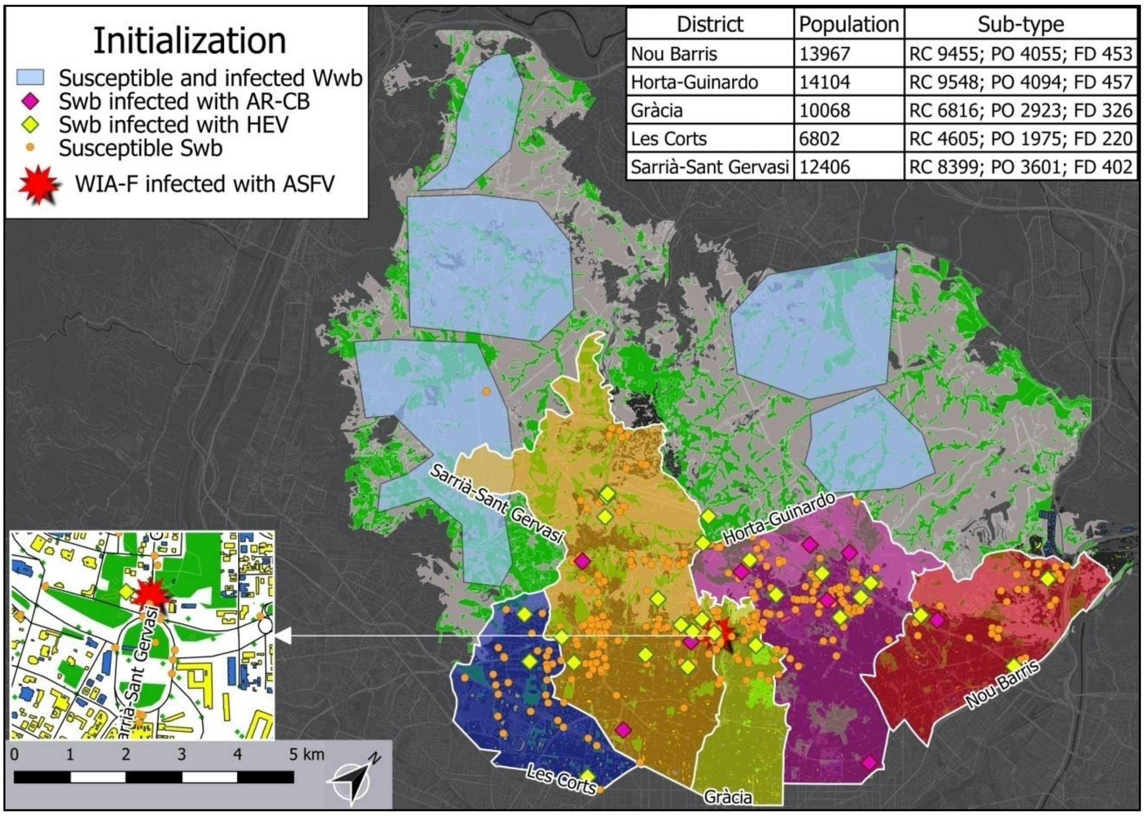


Figure 5.18. Initial location of the susceptible and infected synurbic-wild boar agents (Swb) and non-urban wild boar agents (Wwb) in the (a) AR-CB, antimicrobial resistant *Campylobacter* scenario, (b) HEV, Hepatitis E virus scenario. Initial location of the infected WIA-F agent in the AFSV, African swine fever virus scenario. Number of citizen agents by sub-type (RC, regular citizen; PO, pet owner; FD, feeder citizen), modeled in each district.

In the (1) HEV and (2) AR-CB scenarios, both simulations began with an initial number of infected Swb and Wwb agents, according to the prevalence registered by previous studies, 20% for HEV and 60.8% for *Campylobacter* (Castillo-Contreras, 2019; Wang et al., 2019). Likewise, an initial number of citizen agents at risk (Is_atRisk) were set according with publicly available data. In the (3) ASFV scenario, the simulations started with a single infected WIA-F, located in a WB presence hotspot in the urban area according to the WB locations reported by the local police of Barcelona.

c.2) Input data

Infected Swb and Wwb were initialized in the location where the WB was hunted or captured (GPS data), included as geographical vector files in shapefile format (ESRI1998). Non infected Swb were initialized according to a geolocalized dataset of 400 citizen phone calls related to WB presence in the urban area of Barcelona registered by the Barcelona local police during 2019, which are considered as a reliable proxy of Swb presence (Castillo-Contreras et al., 2018).

The pathogen prevalence's were obtained from previous studies in the BMA area for AR-CB (Castillo-Contreras, 2019; Navarro-Gonzalez et al., 2018) and HEV (Wang et al., 2019).

The input data for the number of citizen agents and the proportion at risk (Is_atRisk) was collected from demographic (Ajuntament de Barcelona, 2019) and public health (Agència de Salut Pública de Barcelona, 2018). publicly available data, respectively.

The remaining epidemiological data used in the model were collected from literature review on WB epidemiological values. Transmission rates from WB to humans were not available in scientific literature, thus, the model used data from experimental infections in other species. In the HEV scenario the data originated from a study about the course of HEV infection in domestic pigs (daily transmission rate of 0.66, (Bouwknegt et al., 2009)), and in the AR-CB scenario the data originated from a study about the transmission dynamics of *Campylobacter jejuni* among broilers (daily transmission rate of 0.13, (Neves et al., 2019)).

c.3) Sub-models

c.3.a) Epidemiological sub-model (EP)

The EP (Figure 5.19) executed the epidemiological processes involved in the human-WB interactions and environmental transmissions taking place in WIAs. All WB agents that were not exposed, infected or resistant were in a susceptible status, as well as the citizen agents, who were initially all susceptible or non-exposed.

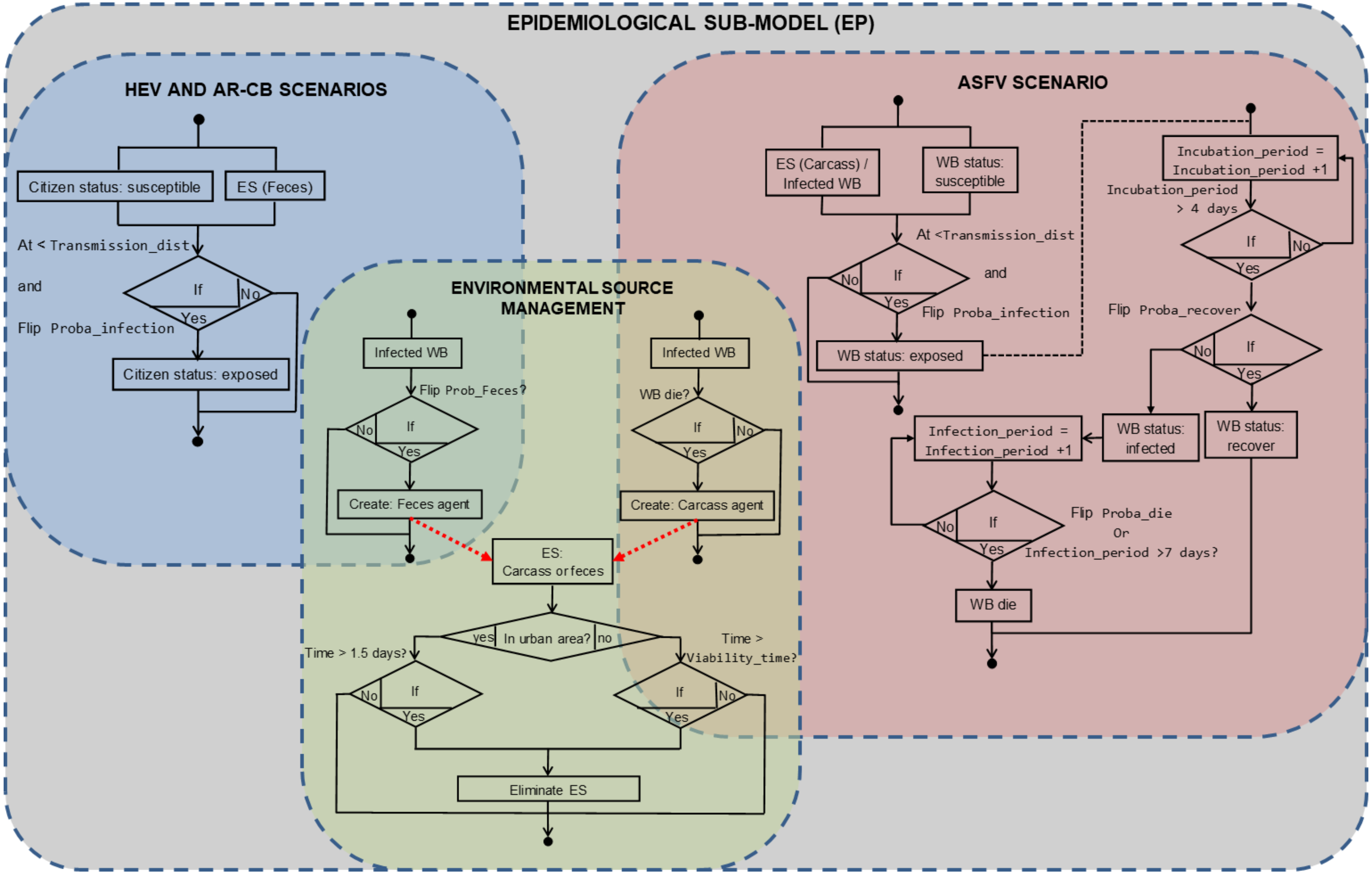


Figure 5.19: Flow chart diagram of the epidemiological sub-model of the BCNWB-EPI model.

- *Exposition and Infection*

Infected WB agents could transmit the pathogen to other WB, either directly or by means of a contamination event producing an ES (feces or carcasses), and to citizen agents. ES, in turn, could further transmit the pathogen to other WB and citizen agents with a given probability. Every infected WB or ES agent computed the total of susceptible agents within the transmission distance, and then, the infection process repeated for each susceptible agent found. The transmission probability depended on the pathogen hosted by the infected agent. If the transmission event took place successfully, the susceptible agent changed the susceptible status to exposed (Is_Exposed). In WB agents, the incubation period was set at zero and increased with each time step until the period for each pathogen elapsed; then, the exposed WB agents changed their status to infected (Is_Infected). ES could happen in each step of the simulation (i.e. when an infected WB agent defecated for HEV and *Campylobacter*, or died for ASFV), immediately starting the transmission process of the pathogen. In each step of the (1) HEV and (2) AR-CB scenarios, infected WB agents had a 0.25 probability of creating an ES agent representing feces (Prob_Feces). In the (3) ASFV scenario, when an infected WB agent died, an ES agent was created in its place, representing the carcass. The information regarding the transmission events and ES creation was stored into a list and the grid agent and used for results, validation and calibration. In the (1) HEV and (2) AR-CB scenarios, at the end of the simulation the number and location of the expositions of citizen agents to the pathogens was used to evaluate the risk of infection for the human population of Barcelona.

- *Recover/Die*

In the (3) ASFV scenario, only 0.5% of the infected WB agents could recover and become resistant (Is_Resistant) but inasmuch as95.5% of the infected WB agents died after 5-11 dpi. A probability of dying, randomly assigned between these values and evaluated in each step of the simulation, was assigned to each ASFV infected WB agent.

- *ES management*

In all three scenarios, ES agents were removed after a time defined by their location. In the natural ecosystem the removal time was in agreement with the survival time of the pathogen in the environment. Conversely, in the urban ecosystem the ES were removed in a shorter time, 1.5 days, capturing the street cleaning services by the city council.

3.3.3.3. Temporal and spatial analyses of model outputs

The BCNWB-EPI model stored in the grid agent (spatial data) the number of ES (feces or carcasses) and the number of direct and indirect transmission events in each cell, and stored in a list (temporal data) the number of transmission events taking place in each step of the simulation. To evaluate the spatial and temporal distribution of the predicted results, the number of feces stored in the grid was corrected by the time extent of the simulation and the surface, and used to calculate the annual probability of finding feces in each city district included in the model. Also, the number of transmission events stored in the list and the grid were used to calculate the probability of citizen exposition for each day of the week, Monday to Sunday, and city district, respectively. Then, statistical analyses on the temporal and spatial distribution of the predicted results were performed using R 4.0.3 (R Core Team, 2020) with the lme4 package developed by (Bates et al., 2015), by means of general lineal models (Poisson distribution) and Tukey tests.

5.3.4. Model results and evaluation

5.3.4.1 Validation

In the (1) HEV and (2) AR-CB scenarios, the sub-model was validated by comparing the number of exposed citizens at the end of the simulation with WHO reports of annual exposition for HEV (World Health Organization 2020b) and AR-CB (World Health Organization 2020a). In the (3) ASFV scenario, validation was performed by comparing the basic reproduction number calculated by the sub-model and the number of resistant WB at the end of the outbreak with previously reported outbreaks for ASFV. The results of the model showed high accuracy in relation to the data used for validation. The model was considered validated when the results were within the range or less than 10% of difference from the data used for validation.

The model was able to spatially simulate the transmission of the modeled pathogens in a timely manner during the study period, accounting for (1) the differential effects of the epidemiological values selected foreach pathogen scenario; (2) the potential impact of ASFV on population dynamics; and (3) the effect on public health of the human-WB interactions in the urban area of Barcelona.

- **(1) HEV scenario**

In the HEV scenario, the model predicted that 452 (i.e., 0.79% of the modeled population) citizen agents (67 considered to be citizens at risk) contacted the pathogen after 365 simulated days. The results of the model agreed (the predicted data were within the range of the validation data) with WHO estimations of 480 humans exposed annually for the modeled population (0.8 for every 100 humans) (World Health Organization 2020b). Figure 5.20 shows the distribution of wild boar feces carrying HEV and the probability of a citizen to be exposed to them in the study area.

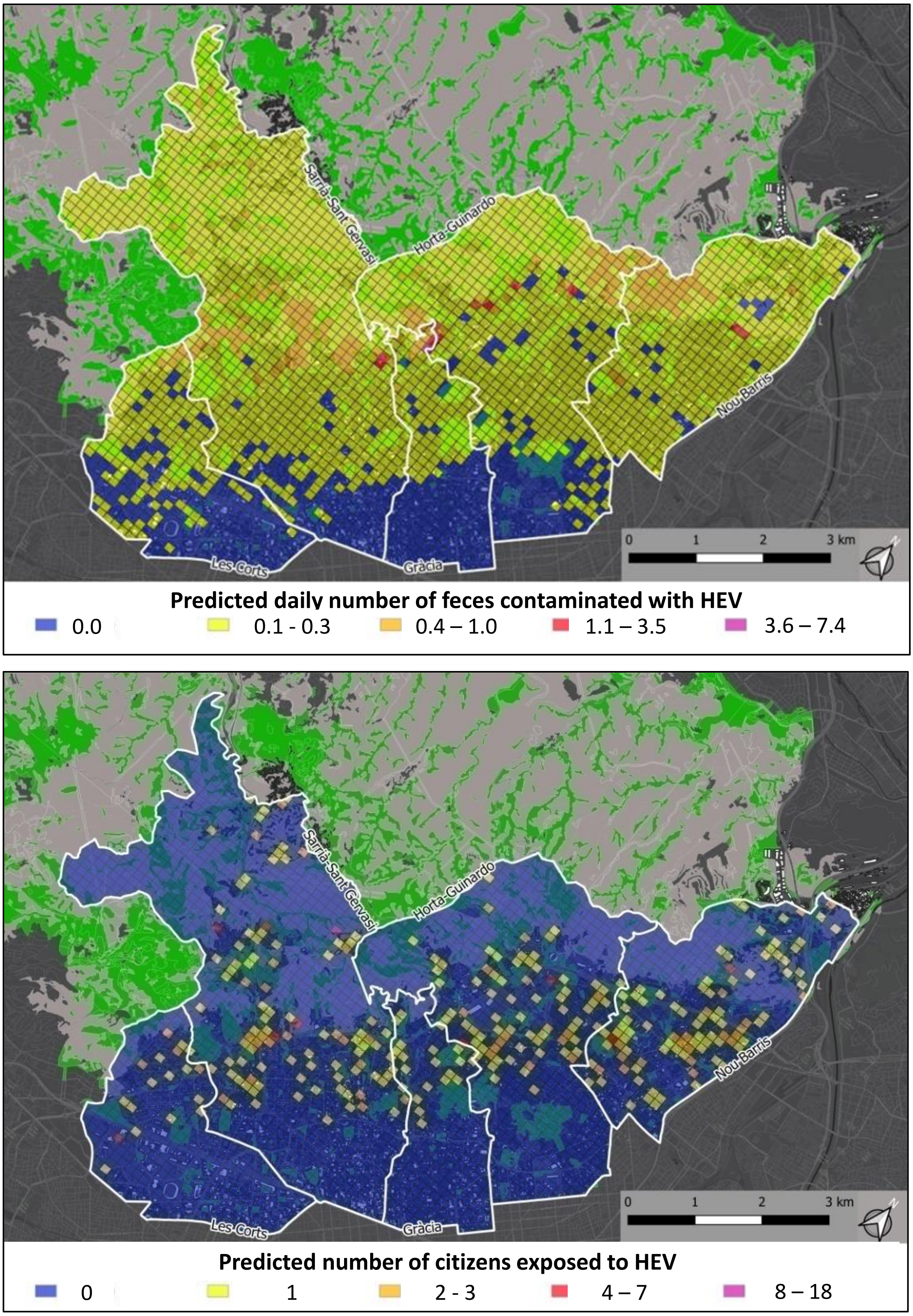


Figure 5.20. Up, Daily number of feces; and Down, Number of citizens exposed over the study period predicted by the Hepatitis E virus (HEV) scenario.

- **(2) AR-CB scenario**

In the AR-CB scenario, the model predicted that 461(i.e., 0.80% of the modeled population) citizen agents (55 considered to be citizens at risk) contacted AR-CB after 365 simulated days. The results of the model agreed (the predicted data were within the range of the validation data) with the annual human exposition to AR-CB estimated by WHO4.4 to 9.3 for every 1000 humans, i.e. from 264 to 558 for the modeled population, (World Health Organization 2020a). Figure 5.21 shows the distribution of wild boar feces carrying AR-CB and the probability of a citizen to be exposed to them in the study area.

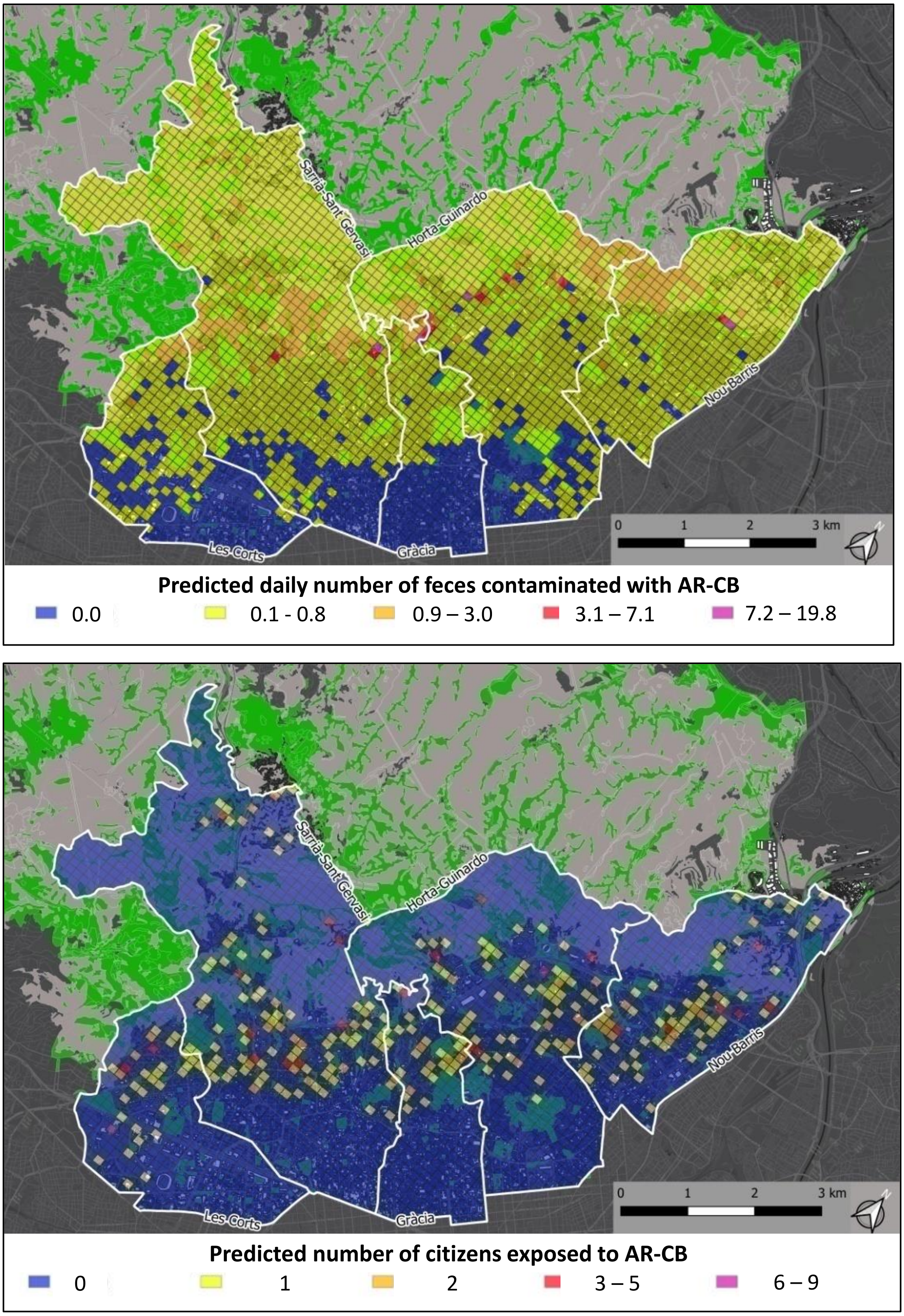


Figure 5.21. Up, Daily number of feces; and Down, Number of citizens exposed over the study period predicted by the antimicrobial-resistant *Campylobacter* (AR-CB) scenario.

(3) ASFV scenario

In the ASFV scenario, the entire WB population in the CNP (including Swb and Wwb agents) was exposed to the virus 51 to 71 days after the index case (Figure 5.22). The transmission of ASFV within the WB population was mediated by carcasses in 87.6% of the cases and by direct contact in the remaining 12.4% of the cases. The outbreak lasted between 71 and 124 days, reducing 95% of the initial population. The model calculated a basic reproduction number (R_0) of 16.9 for the simulated ASFV pathogen. The results of the model agreed (the predicted data were within the range of the validation data) with the R_0 estimated in previously reported ASFV outbreaks, from 4.4 to 17.3 (Guinat et al., 2018). Figure 5.23 shows the distribution and number of direct and indirect ASFV transmission events in the study area.

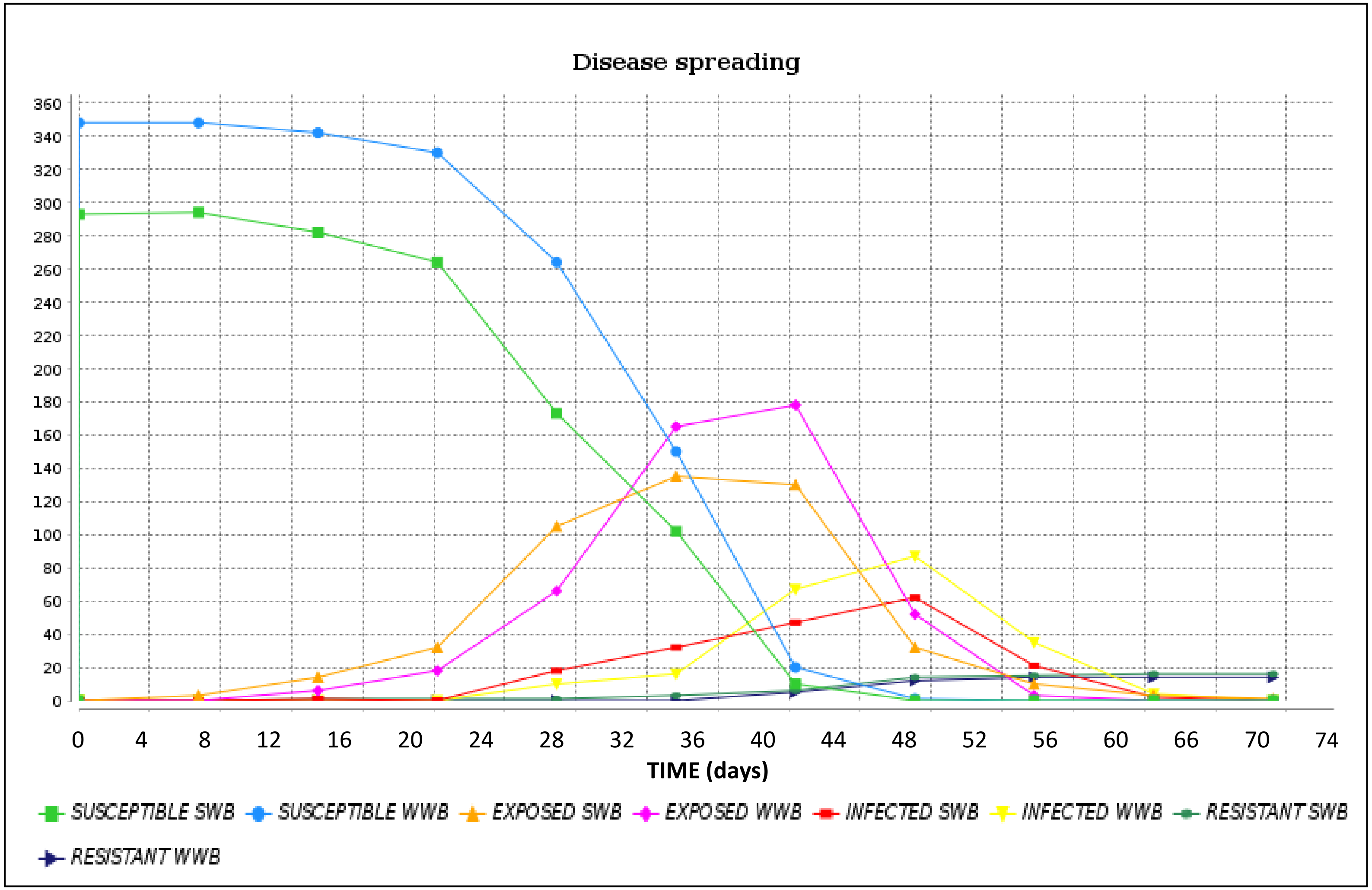


Figure 5.22. Dynamics of the African swine fever virus outbreak in the wild boar population modeled. Each line shows the number of susceptible, exposed, infected and resistant non-urban wild boars (Wwb) and synurbic wild boars (Swb) agents.

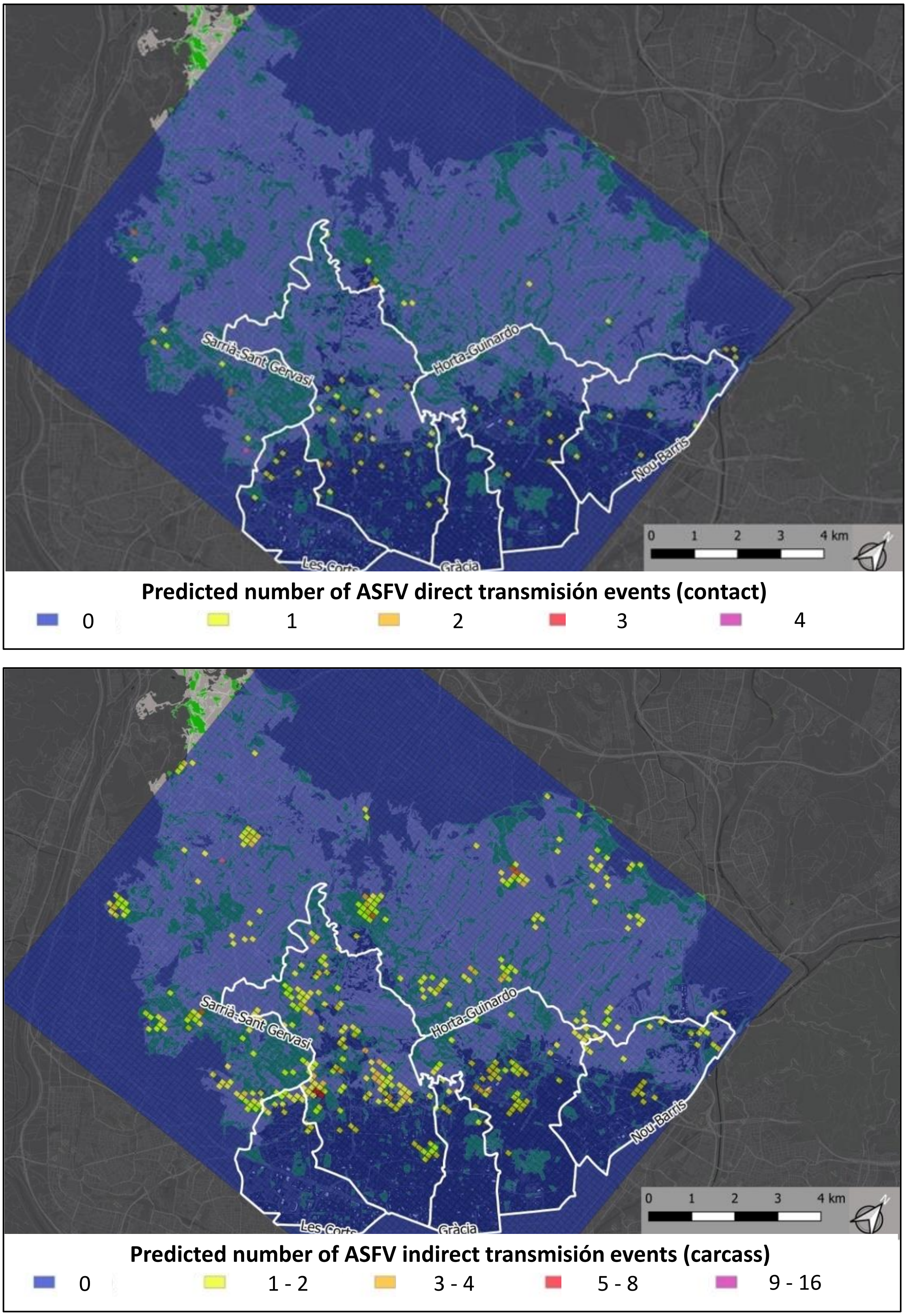


Figure 5.23. Location and number of ASFV transmission events over the study period predicted by the African swine fever (ASFV) scenario. Up, Direct transmission events between WB agents; Down, Indirect transmission events from carcasses to WB agents

5.3.4.2 Temporal distribution

The number of transmissions events predicted varied significantly depending on the day of the week (Monday to Sunday; Table 5.9) and over the study period (Figure 5.24).

Table 5.9. Predicted temporal distribution of the probability of citizen exposition..

	Citizen exposition	
Day	**Hepatitis E virus scenario**	**Antimicrobial resistant *Campylobacter* scenario**
Monday	0.8868^{b}	2.0189^{a}
Tuesday	0.1731^{c}	1.1346^{b}
Wednesday	0.2500^{c}	1.0192^{b}
Thursday	1.4423$^{a\text{-}b}$	0.3269^{c}
Friday	1.2692^{b}	0.3846^{c}
Saturday	2.2115^{a}	1.0962^{b}
Sunday	2.4423^{a}	2.8462^{a}
	F_6:24.127, p:<0.0001	F_6:27.338, p:<0.0001

$^{a, b, c}$ Values with different superscripts are different (p <0.05) within each column.

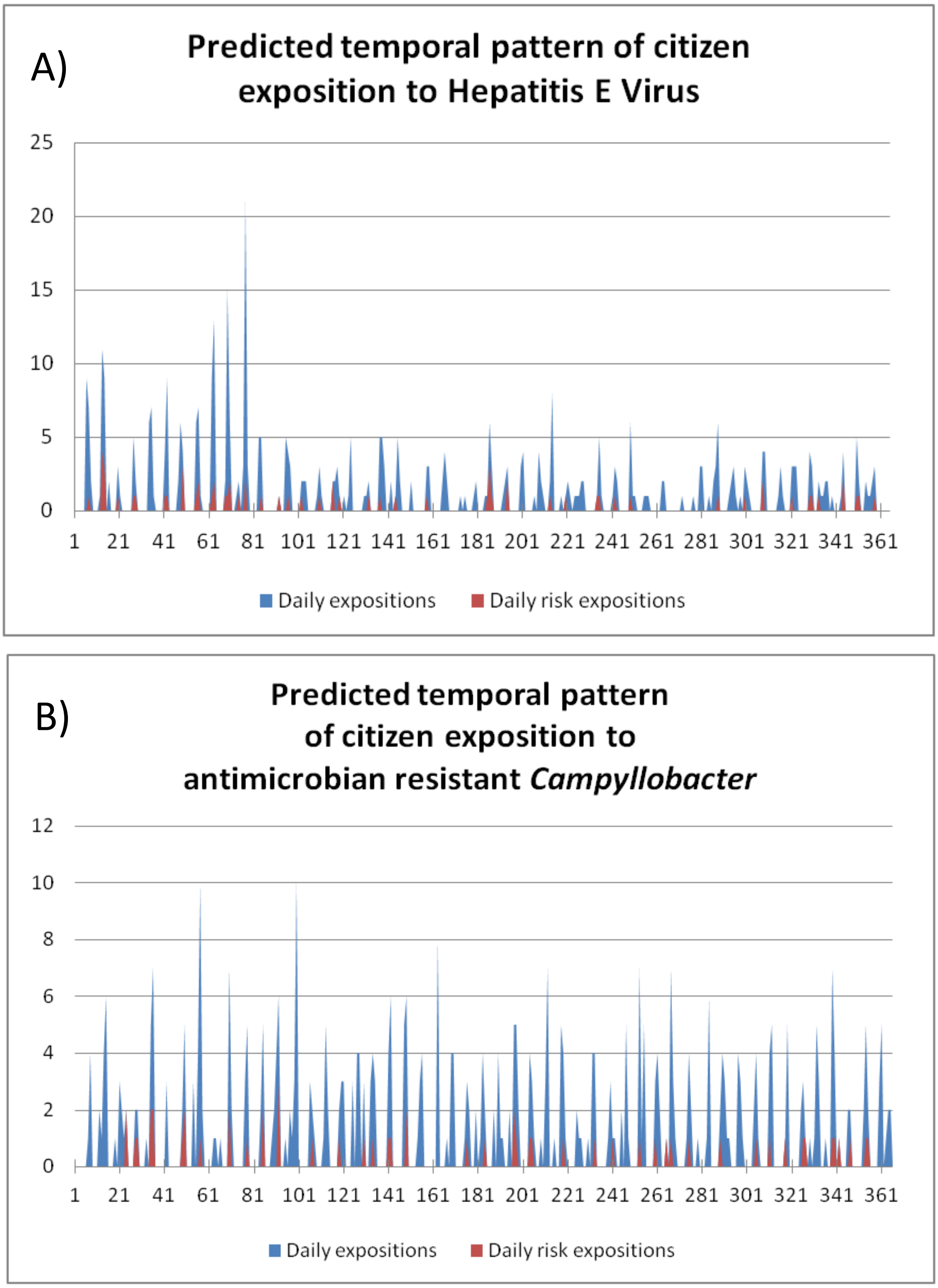


Figure 5.24. Daily citizen exposition over the study period to A) Hepatitis E virus (HEV); and B) antimicrobial-resistant *Campylobacter* (AR-CB), predicted by the HEV and AR-CB scenarios, respectively.

5.3.4.3 Spatial distribution

The spatial distribution of the predicted results evidenced statistically significant differences among the districts in the presence of feces carrying pathogens (AR-CB scenario F_4:18.712,p: <0.0001; HEV scenario F_4:7.258,p: <0.0001) and citizen expositions to such feces (AR-CB scenario F_4:3.061,p: 0.0156; HEV scenario F_4:14.798,p: <0.0001) among districts (Table 5.10).

Table 5.10. Predicted spatial distribution of the annual probability of feces carrying *Campylobacter* or hepatitis E virus and citizen exposition to them in the five urban districts of the study area.

	Hepatitis E virus scenario		**Antimicrobial resistant *Campylobacter* scenario**	
District	**Daily number of feces**	**Citizen exposition**	**Daily number of feces**	**Citizen exposition**
GRÀCIA	$0.0878^{a\text{-}b}$	$0.0860^{b\text{-}c}$	0.2343^{b}	$0.1505^{a\text{-}b}$
HORTA-GUINARDÓ	0.1332^{a}	0.1372^{b}	0.3809^{a}	$0.1346^{a\text{-}b}$
LES CORTS	0.0379^{b}	0.0707^{c}	0.1293^{c}	0.1195^{b}
NOU BARRIS	0.1371^{a}	0.2556^{a}	0.3445^{a}	0.1903^{a}
SARRIÀ-SANT GERVASI	0.1359^{a}	0.1441^{b}	0.3864^{a}	0.1300^{b}
	F_4:14.798, p: <0.0001	F_4:7.258, p: <0.0001	F_4:18.712, p: <0.0001	F_4:3.061, p: 0.0156

[a, b, c] Values with different superscripts are different (p <0.05) within each column.

5.3.5. Discussion

This model provided the first modeled information on the zoonotic HEV and AR-CB hazard posed by WB in the urban area of Barcelona, as well as the epidemiological and WB PD consequences of an ASFV outbreak in the urban and (peri)urban WB population of Barcelona and Collserola. The model not only reflected the total number of humans exposed to these zoonotic pathogens and the dynamics of the potential WB ASFV epidemics numerically, but also allowed the identification of the more relevant locations for transmission within the WB population and to humans (Figures 5.5 and 5.6).

(1) HEV scenario and (2) AR-CB scenario

Although the prevalence of the two zoonotic pathogens modeled was different and the model/sub-model/module captured the differences in the trend and human exposition dynamics the number of citizens exposed to the pathogen after a year was similar. This suggests a major role of feces in the transmission of HEV and AR-CB from WB to humans in urban and (peri)urban environments, resulting consequently in a public health risk with associated implications in the management of wildlife in the urban ecosystem. Although the model/sub-model/module included a shorter life-time of feces in the urban area as compared to the (peri)urban locations due to street cleaning services, still human exposition events took place in the urban area (Figures 5.5 and 5.6). This indicated the relevance of WB presence and derived contamination in urban areas as a key driver in the epidemiology of zoonotic pathogens (Ruiz-Fons, 2017) in the new human-Swb interface (Becker et al., 2015, 2018; Meng et al., 2009).

The BCNWB-EPI model predicted in the HEV and AR-CB scenarios an accumulation of transmission events around the weekend, particularly in the HEV scenario. This weekly pattern in AR-CB and HEV thus probably results from the increased human-WB interactions in WIAs during the weekend, when citizens use more often and intensively the green areas and tracks in the CNP. The daily average number of feces contaminated with HEV and AR-CB was positively associated with human population numbers. The three-fold higher average probability for AR-CB than for HEV can probably be related to the different prevalence of these pathogens in the WB population. The highest predicted risk to AR-CB and HEV in NOBA may be associated with a higher infiltration of WB in the urban area of the district. Conversely, the lowest predicted risk to HEV in LCOR and GRA, on the one hand, and in LCOR and SSGE for AR-CB, on the other hand, may be associated with a smaller border area with CNP (LCOR and GRA) and with a lower human population density (LCOR and SSGE), respectively.

(3) ASFV scenario

The ASFV scenario evidenced the repercussions of experiencing an ASFV outbreak resulting from the presence of WB in urban areas, as a consequence of the feeding behavior from anthropogenic resources, where in most countries pig/WB meat products can be usually found. Following the case of Czech Republic with a single point of introduction of ASFV to WB (Šatrán, 2017) a single WB agent contacting a contaminated WIA-F agent, representing leftovers with infected pig meat, was the origin of the simulated outbreak. The model simulated a real case scenario in the city of Barcelona, a waste container near a well-frequented gas station and located in one of the areas with higher WB presence registered by the BCNPD. The model predicted a rapid spread of ASFV within the WB population, probably resulting from the virtual isolation of the CNP from the nearest natural areas and therefore other WB populations, a relative high density of the WB population (Depner et al., 2017), an increased contact rate due to aggregation in the anthropogenic food resources concentrated in human areas (Becker et al., 2015, 2018; Swift et al., 2019) and the role of Swb and carcasses as drivers in local propagations. Carcasses were predicted to be the main source of transmission events (Depner et al., 2017; Dixon et al., 2019; Khomenko et al., 2013; More et al., 2018; Sánchez-Cordón et al., 2018); on one hand the virus have an increased survival conditions, and on the other hand WB are attracted to carcasses, whether or not intraspecies predation or scavenging occurs (Khomenko et al., 2013; Probst et al., 2017).

Overall, the findings highlight the role of ES in the spread of the studied pathogens. According to the prediction of the model, probably the most efficient mitigation strategy to reduce the epidemiological risk of outbreak and/or spillovers to humans would be reducing the presence of WB in urban areas (Hassell et al., 2017; Meng et al., 2009; Ruiz-Fons, 2017), the systematic elimination of ES and decreasing the contact of citizens with ES and WB. The strategy to specifically reduce the public health risk posed to the citizens of Barcelona by ES contaminated with HEV and AR-CB, should combine the reduction and elimination of WB feces in urban areas, especially in green areas, with an awareness campaign to inform about the epidemiological risk of WB and ES. To reduce the animal health risk posed by ASFV to the WB population in CNP, WB accessibility to anthropogenic resources should be limited, especially waste containers (Becker et al., 2018; Costard et al., 2009; Sánchez-Cordón et al., 2018). In the case of an ASFV outbreak, a prompt response strategy aimed at reducing the contact of susceptible WB with infected ES, mainly WB carcasses, should be established. The efforts should be increased to locate and eliminate every single carcass and, due to the high mobility and dispersal capabilities of synurbic WB, it is highly recommended to cull every WB in the (peri)urban area (Costard et al., 2009; Depner et al., 2017; More et al., 2018; Rowlands et al., 2008). The model can be used as a decision platform in the management of the WB population by the local administration, to evaluate the epidemiological risk posed to public health of zoonotic pathogens hosted by the WB population in the CNP.

Altogether, BCNWB-EPI model provided evidence of the wildlife–pathogen dynamics response to synurbization and foraging on anthropogenic resources unintentionally provided in urban habitats. Due to the concentration of food resources and the consequent decrease in home range (Luniak, 2004; Tucker et al., 2020), synurbic animals experience an increase in host aggregation and overlap between wildlife and spillover hosts, resulting in an increase in host exposure and susceptibility to pathogens (Becker et al., 2015, 2018). The model predictions demonstrated the potential epidemiological risk and the role as disease reservoir (Meng et al., 2009; Ruiz-Fons,

2017) of synurbic WB in urban areas (Lloyd-smith et al., 2009) for the WB population and spillovers to humans. The mediating role of anthropogenic resources, feces and carcasses, in the maintenance and circulation of pathogens and in the spatial spread of infection is to be acknowledged in the light of the results of this study (Becker et al., 2018; Costard et al., 2009; More et al., 2018; Probst et al., 2017; Ruiz-Fons, 2017; Sánchez-Cordón et al., 2018)The characteristics of synurbic WB and ES increase pathogen spread along the space and through time, therefore increasing the probability of the pathogen to contact susceptible WB and human hosts. Spatially, synurbic WB have an increased probability to contact the pathogen when feeding from anthropogenic resources (Becker et al., 2015, 2018), and the ability to move between the natural and urban ecosystems, contacting in the process other susceptible WB and humans. Temporally, the ES favor the aggregation of multi-species susceptible host.

This study brings a new contribution to epidemiology and urban wildlife management using spatially explicit ABM, which was able to capture and analyze the complexity of the epidemiological processes of three pathogens in the human-wildlife interface, at small-scale and in the context of the BMA. In order to do so, the model considered multiple environmental, epidemiological and biological variables, and fine scale space and time were explicitly modeled. This is not only a more realistic spatial-temporal framework, but also allowed an independent environment dynamic. Moreover, WB and citizen agents programming captured the spatial and temporal (daily and weekly) human and WB activity in the urban and natural ecosystems ((Alfeo et al., 2019; Alonso et al., 2018; Grignard et al., 2018), Study 2) of the BMA.

Some limitations of this model were related to the model calibration and validation due to the lack of information in scientific literature of the epidemiological processes of zoonotic pathogens, with uncertainties regarding transmissibility to the human population and accurate estimates of population exposition at regional level. Although there were experimental infection studies for HEV and ASFV in pigs and WB (Bouwknegt et al., 2009; Cook & van der Poel, 2015; Guinat et al., 2016), that was not the case for *Campylobacter*, where the epidemiological studies available originated mostly from the poultry industry (Neves et al., 2019). The lack of data may have resulted in an overestimation of the transmission rates; the decision was based on the need to maximize citizen exposition, in an attempt to include the worst-case scenario in the risk assessment of each pathogen. However, the coincidence of the model/sub-model/module output with the estimated ranges provided by the WHO is an indicator that real values are likely close to the model/sub-model/module predictions.

5.3.6. Conclusion

The seriousness of SARS-CoV-2 underlines the need of the promotion and further implementation of the “One Health Approach” (Rabozzi et al., 2012; Zinsstag et al., 2005) and the interdisciplinary cooperation among animal, public and environmental health. As urbanization continues expanding, the risk of outbreaks of emerging diseases resulting from human-wildlife interactions (HWIs) are likely to continue increasing. Prevention is based on knowledge, but predicting zoonotic diseases outcomes is extremely difficult and poorly understood due to the constantly evolving nature of the multiple factors involved (Rabozzi et al., 2012), varying on a case–by-case basis. However, the onset of infections may be anticipated as a result of the correlation with environmental factors (Rabozzi et al., 2012). To design surveillance systems and enhanced diagnostics of emerging pathogens under new approaches (McMichael, 2004; Rabozzi et al., 2012), priority must be given to improve the knowledge about the pathogens, including vectors and reservoirs, and the complexity of the ecosystem, including temporal and spatial relationships),by examining current zoonotic diseases (McMichael, 2004).The present study demonstrates the efficacy of ABM as an epidemiological decision-making tool adapted to the circumstances of the study area. The prediction generated by the model can be used to: (1) anticipate the location of the pathogen; (2) inform health risk assessments to evaluate the animal and public health risk posed by the spread of these pathogens; and (3) design appropriate control measures, to prevent the appearance and control the spread of the pathogen (McMichael, 2004). The integration of urban biologists with human and animal health epidemiologists and health care professionals in urban development planning and management is essential to reduce unwanted HWIs and the consequences risk of zoonosis transmission.

6. DISCUSSION

This thesis provides insights into the drivers of WB dynamics in CNP and the most effective management strategies to reduce WB population density (Study 1). Also, the SES driving the use of the urban ecosystem by synurbic WB and the human-WB interactions in the (peri)urban area of Barcelona are analysed (Study 2). Finally, the epidemiological risk posed by WB in the (peri)urban area of Barcelona is evaluated, quantifying and spatially locating their role in the maintenance, circulation and spatial spread of pathogens (Study 3).

4.1. Drivers and management of WB population dynamics in (peri)urban environments

Food availability was identified as the main driver for population size, followed by the mortality rate of juvenile and yearling females. The supplementary anthropogenic food resources available to WB in the (peri)urban areas surrounding and within the CNP has most probably tripled (Study 1) the natural CNP carrying capacity (Cahill et al., 2012a; Cahill & Llimona, 2004). Summer is the period with highest mortality of WB in Mediterranean populations due to the natural scarcity of food and water (Massei & Genov, 1997), but supplementary feeding, irrigated green areas and artificial fountains provide food, water and thermoregulation for WB, thus avoiding the natural constraints of foraging on demographic effect (Choquenot & Ruscoe, 2003). In the CNP population, the incidences in urban areas are mostly caused by juveniles and females with piglets in good nutritional conditions during summer (Castillo-Contreras et al., 2018), suggesting that the availability of anthropogenic resources in (peri)urban areas compensate the natural environmental constraints. The higher effect of juvenile and yearling mortality on population dynamics is likely related to the increased offspring production (through an advance of first reproduction and an increase in body condition favoring higher fetal numbers), piglet survival and population recruitment, due to the overabundance of anthropogenic resources in CNP and the AMB. The anthropogenic food available with the consequent reduction in mortality in juveniles and yearlings and the capability of WB of exploiting these resources, explain the increasing trend observed in the CNP WB population.

When assessing the most efficient and effective management measures, decreasing food availability had the strongest total effect, whereas selective harvesting of juveniles and yearlings was more effective and easier to implement. Moreover, the combination of decreasing carrying capacity by reducing supplementary anthropogenic food and focusing population control on the age categories most relevant demographically (i.e., juveniles and yearlings) revealed as the most efficient and effective management strategy, achieving control an increasing WB population in a Mediterranean (peri)urban environment with supplementary food over the natural resources. Although reducing juvenile and yearling population might be more challenging than reducing adult WB population, focusing on juveniles and yearlings allows a lower number of WB to be harvested to control population growth, therefore including also benefits from the animal right and welfare perspective.

Anthropogenic food resources have been previously reported as attracting factors for WBs in urban areas such as Barcelona in Spain (Cahill et al., 2012a; Castillo-Contreras et al., 2018), Haifa in Israel (Toger et al., 2018) and Crackow in Poland (Podgórski et al., 2013). Such resources create the SES driving the use of the urban ecosystem by synurbic WB (Study 2, (Lischka et al., 2018)), as well as the human-WB interactions and associated consequences in the (peri)urban area of Barcelona (Study 2 and Study 3) and other urban contexts (Podgórski et al., 2013; Toger et al., 2018). Therefore, decreasing supplementary feeding provided by anthropogenic resources is crucial for the management of human-WB conflict in (peri)urban areas, involving natural, environmental and social factors (Study 2).

Although suggested as a potential population management measure, decreasing the percentage of breeding females did not seem a feasible target for reducing the CNP WB population, since required restraining the percentage of adult breeding females below 30% in order to appreciate significant effects on population size. Future approaches to fertility control achieved through feeding may be able to more feasibly target a higher proportion of the population, thus making fertility control a management option in restricted areas closed to WB movements, such as urban or protected areas.

4.2. WB populations in the social-ecological systems (SES) of (peri)urban areas

The spatial prediction of WB presence in urban areas and the associated human-WB conflicts obtained by the BCNWB model (Study 2) captured the SES of the urban ecosystem of Barcelona. In such (peri)urban contexts, anthropogenic food resources and human behavior (Study 1) are the main drivers of the use of the habitat by synurbic

WB (Castillo-Contreras et al., 2018) and the associated human-WB interactions and conflicts (Study 2 and Study 3). Altogether, suggest that synurbic WBs of the CNP prioritize closer anthropogenic food resources according to the optimal foraging theory (Morelle et al., 2015; Spitz & Janeau, 1990; Stephens & Krebs, 2020).

For a WB presence to be recorded by the local police, first both a citizen and a WB must be present at the same time and place; then a human-WB interaction must occur (Study 2 and Study 3), and, finally, a citizen has to report it to the police. The higher value of WB presences predicted by the BCNWB model (Study 2) as compared to those registered by the BCN police department (3.5:1 ratio) could be explained by the aforementioned detectability and report requirements. Therefore, the actual presence of WB in the urban area of BCN could be closer to the values provided by the model, the values recorded by the local police being a good proxy provided human activity and citizen habituation to WB presence in the urban area do not change significantly (Conejero et al., 2019). The current movement restrictions caused by the COVID-19 pandemics must be consequently considered when interpreting WB interactions report in the future, since they significantly affect human mobility and therefore the detectability of WBs by people.

4.3. Epidemiological consequences of WB synurbization

Due to the concentration of food resources and the consequent decrease in home range (Becker et al., 2018; Luniak, 2004; Tucker et al., 2020), synurbic animals (including WB, but also black bear (*Ursus americanus* (Lischka et al., 2018)), Chacma baboon (*Papio hamadryas ursinus* (Kansky et al., 2016)), raccoon (*Procyon lotor* (Prange et al., 2004)), key deer (*Odocoileus virginianus clavium* (Harveson et al., 2007)) or stone marten (*Martes foina* (Herr et al., 2009)) experience an increase in population density (Study 1), aggregation and territorial overlap between wildlife and spillover hosts (i.e. humans, Study 2). This results in an increase in host exposure and susceptibility to pathogens (Becker et al., 2015, 2018; Luniak, 2004), as well as an increased circulation of density- and contact-dependent pathogens (Hassell et al., 2017; Haydon et al., 2002; Lloyd-smith et al., 2009). Altogether, the BCNWB-EPI model (Study 3) provided evidence of the wildlife–pathogen dynamics response to synurbization and foraging on anthropogenic resources (Study 1 and Study 2). The model predictions demonstrated the potential epidemiological zoonotic risk and the role as disease reservoir of synurbic WBs in urban areas, as demonstrated in rural environments (Ruiz-Fons, 2017). However, the higher interspecific human-WB contact (either direct or indirect) in urban areas enhances the risk of pathogen transmission and circulation at the WB-human interface. As urbanization continues expanding, the risk of outbreaks of emerging diseases resulting from HWIs are likely to continue increasing.

Although the BCNWB-EPI model captured the differences in the trend and human exposition dynamics between HEV and AR-CB (Study 3), the number of citizens exposed to each pathogen after a year was similar. This indicated the relevance of environmental sources of contamination (i.e. feces) as a key driver in the epidemiology of zoonotic pathogens (Ruiz-Fons, 2017) in the (peri)urban human-synurbic WB interface (Becker et al., 2015, 2018; Hassell et al., 2017; Lloyd-smith et al., 2009). The resulting public health risk has implications in the management of wildlife in urban ecosystems. The characteristics of the Barcelona-CNP ES influenced the epidemiological predictions, since differences in the infiltration of WBs in the district area, the surface of the border area between the natural and the urban environments, and human population density of the district may be associated with differences in the risk of human exposition to feces contaminated with AR-CB and HEV. Moreover, the weekly pattern found in the HEV and AR-CB scenarios probably results from the increased human-WB interactions (Study 2) in WIAs during the weekend, when citizens use more often and intensively the green areas and paths in the CNP.

Similarly, an increased contact rate due to the relative high density of the CNP WB population (Depner et al., 2017) and their aggregation in anthropogenic food sources in (peri)urban areas (Study 2, (Becker et al., 2018; Hassell et al., 2017; Ruiz-Fons, 2017; Tucker et al., 2020)) could explain the rapid predicted spread of ASFV within the WB population. The role played by feces in the zoonotic interspecific transmission of HEV and AR-CB as the main source of transmission events, corresponds to Swb and carcasses in the intraspecific transmission of ASFV (Depner et al., 2017; Dixon et al., 2019; Khomenko et al., 2013; Lange & Thulke, 2017; Probst et al., 2017; Sánchez-Cordón et al., 2018). Moreover, the relative isolation of CNP from the nearest natural areas may contribute to enhance the circulation of pathogens such as ASFV in a closed WB population.

Although WB is acknowledged as a reservoir for zoonotic diseases and diseases shared with livestock, the particularities of synurbic WB and the (peri)urban ES increase pathogen spatial spread and duration, therefore increasing the probability of the pathogen to contact susceptible WB and human hosts (Hassell et al., 2017; Lloyd-smith et al., 2009; Meng et al., 2009; Tucker et al., 2020). Spatially, synurbic WB have an increased probability to contact the pathogen when feeding from anthropogenic resources (Becker et al., 2015, 2018), and the ability to move between the natural and urban ecosystems. Temporally, the ES favor the aggregation of susceptible hosts and increase pathogen survival. The feeding behavior of synurbic WBs from anthropogenic resources in urban areas, where pig and/or WB-derived products can be found, favor the possibility of the acquisition of ASFV from anthropogenic resources at the urban human-synurbic WB interface. Overall, the human-WB contact and the WB aggregation and density in (peri)urban SES enhance the risk of acquisition, transmission (both intra and interspecific) and circulation of pathogens.

4.4. Potential applications of models for wildlife research and management

Models such as PVA (Study 1) and ABM (Study 2 and Study 3) are a proved useful tool for wildlife management (McLane et al., 2011). As demonstrated in this thesis, models can be used to indirectly determine carrying capacity, predict population trend, test and target the sensitivity of biological variables and management strategies, and integrate complex social and ecological (environmental and biological) factors over time and space, allowing the inclusion of specific urban biotopes. This permit designing efficient and effective management plans prior to undertaking any action, increasing the effectiveness of management efforts through saving money and resources under the usually limited budgets.

Spatially explicit models (Study 2 and Study 3) include scales of resolution of mechanisms able to simulate the emergence of patterns from small-scale processes. Such processes are fundamental drivers of ecosystems (McLane et al., 2011; Zhang & DeAngelis, 2020), but conventional urban wildlife management strategies usually underestimate their role and ignore their spatial distribution, hence not successfully achieving the management goals, either to promote or to control an urban population. The development and implementation of ABM models can provide a useful decision-support tool that can be easily adapted to other animal species and regions to answer a range of research questions and evaluate interactions, conflicts and disease transmission potential at the wildlife-domestic animal-human interface. This thesis demonstrates the efficacy of ABM as an epidemiological decision-making tool adapted to the SES of the study area. The prediction generated by the model can be used to: (1) anticipate the location of pathogens;(2) inform health risk assessments to evaluate animal and public health risk posed by the spread of these pathogens; and (3) design appropriate control measures, to prevent the appearance and control the spread of the pathogen (Study 3, (Burroughs et al., 2002)).

The results and management applications obtained by the models could serve as a basis for other Mediterranean WB (peri)urban populations, for the management of both WB populations and health risk. The BCNWB-EPI model provided the first spatial explicitly modeled information on the zoonotic HEV and AR-CB hazard posed by WBs in the urban area of Barcelona, as well as the consequences of an ASFV outbreak in the (peri)urban WB population of CNP, identifying the more relevant locations for transmission within the WB population and to humans. This study brings a new contribution to epidemiology and urban wildlife management using spatially explicit ABM, which was able to capture and analyze the complexity of the (peri)urban SES considering multiple environmental, epidemiological and biological variables, fine scale modeling space and time in the context of the BMA. Therefore, the model can be used as a decision platform in the management of the WB population by the local administration, to evaluate the epidemiological risk posed to public health of zoonotic pathogens hosted by the WB population in the CNP. Moreover, the procedure followed to achieve these goals can be used in other synurbic WB populations and also made extensive to other synurbic wildlife-human interfaces involving other wildlife species.

Models, however, have limitations since they are representations of reality and not reality itself. Such limitations are related to the data quality required for model calibration and validation, due to the lack of information in scientific literature. Data such as schedule and location of feeding events, location of WIAs in urban areas, WB presence in non-urban areas, uncertainties regarding pathogen transmissibility between WBs and humans and accurate estimates of human population exposition at regional level were extrapolated from sources on other contexts, therefore increasing the variability of the model output. The seriousness of the SARS-CoV-2 pandemics underlines the need to promote and further implement the “One Health Approach” (Rabozzi et al., 2012; Zinsstag et al., 2005) and the interdisciplinary cooperation among animal, public and environmental health. Prevention is based on knowledge, but predicting zoonotic diseases outcomes is extremely difficult and poorly understood due to the constantly evolving nature of the multiple factors involved [4], varying on a case–by-case basis. However, the onset of infections may be anticipated by analyzing their correlation with environmental factors (Rabozzi et al., 2012). To design surveillance systems and enhanced early diagnostics of emerging pathogens under new approaches (Burroughs et al., 2002; Rabozzi et al., 2012) priority must be given to improve the knowledge about pathogens, including vectors and reservoirs, and the complexity of ecosystems, including temporal and spatial relationships (Burroughs et al., 2002).

4.5 Management implications

The most efficient management strategy to control the increasing WB population of CNP and therefore, reduce the presence of WB in urban areas, as well as the related incidences and zoonotic risk is reducing food availability. To achieve this goal, management efforts should focus on (1) eradicating voluntary feeding; (2) control WB access to stray cat food; (3) improve waste collection systems and schedule; and (4) manage green areas in the CNP and its surroundings, including urban green spaces, to vegetation less attractive for WBs. Increasing night waits under special permits and collective captures would allow specifically targeting the life stages more determinant for WB population dynamics (namely juveniles and yearlings), since they are more selective and efficient than traditional drive hunts [55,56].

The most efficient mitigation strategy to reduce the epidemiological risk of outbreak and/or spillovers to humans would be, besides reducing the presence of WBs in urban areas (Study 1, (Hassell et al., 2017; Meng et al., 2009; Ruiz-Fons, 2017)), the systematic elimination of ES and decreasing the contact of citizens with ES and WBs (Study 2 and Study 3). The strategy to specifically reduce the public health risk posed to the citizens of Barcelona by ES contaminated with HEV and AR-CB, should combine the reduction and elimination of WB feces in urban areas, especially in green areas, with an awareness campaign to inform about the epidemiological risk of WBs and ES. To reduce the animal health risk posed by ASFV to the WB population in CNP, WB accessibility to anthropogenic resources should be limited, especially waste containers and direct feeding (Costard et al., 2009; Sánchez-Cordón et al., 2018). In the case of an ASFV outbreak, a prompt response strategy aimed at reducing the contact of susceptible WB with infected ES, mainly WB carcasses, should be established. The efforts should be increased to locate and eliminate every single carcass and, due to the high mobility and dispersal capabilities of synurbic WB, every WB in the (peri)urban area should be culled (Costard et al., 2009; Depner et al., 2017; More et al., 2018; Rowlands et al., 2008).

5. CONCLUSIONS

1. Anthropogenic food resources increase carrying capacity of urban ecosystems for WB as compared to natural ecosystems.

2. The variables with more impact on the dynamics of the CNP WB population are the carrying capacity and the survival of juveniles and yearlings.

3. Reducing the carrying capacity and increasing mortality of juveniles and yearlings is the most efficient and effective strategy to reduce and control the CNP WB population.

4. Reducing reproduction and increasing mortality on adult WB have a negligible impact on the dynamics of the CNP WB population, except at high rates.

5. Anthropogenic food resources play a major role in the attraction and habituation of WB to urban areas, and act as aggregation points increasing pathogen exposition.

6. The zoonotic pathogens hosted by wild boars in the Metropolitan Area of Barcelona (BMA), suppose a health risk for the wild boar population and the inhabitants of the city.

7. Anthropogenic resources and ES (feces and carcasses) play a mediating role in the maintenance and circulation of pathogens and in the spatial spread of infection.

8. Models such as PVA and ABM are a proved useful tool for wildlife management.

9. ABM can provide spatio-temporal predictions of human-wildlife interactions, conflicts and disease transmission.

7. REFERENCES

Acevedo, P., Escudero, M. A., Muñoz, R., & Gortázar, C. (2006). Factors affecting wild boar abundance across an environmental gradient in Spain. *Acta Theriologica*, *51*(3), 327–336. https://doi.org/https://doi.org/10.1007/BF03192685

Acevedo, P., Quirós-Fernández, F., Casal, J., & Vicente, J. (2014). Spatial distribution of wild boar population abundance: Basic information for spatial epidemiology and wildlife management. *Ecological Indicators*, *36*, 594–600. https://doi.org/10.1016/j.ecolind.2013.09.019

Adams, C. E. (2016). Urban Wildlife Management. In *Urban Wildlife Managment*. CRC Press. https://doi.org/10.7589/0090-3558-43.2.321

Adams, L. W. (2005). Urban wildlife ecology and conservation: A brief history of the discipline. *Urban Ecosystems*, *8*(2 SPEC. ISS.), 139–156. https://doi.org/10.1007/s11252-005-4377-7

Akçakaya, H. R., Burgman, M. A., & Ginzburg, L. R. (1999). *Applied Population Ecology*. http://www.ramas.com/apppopn.htm

Akçakaya, H. R., & Sjögren-Gulve, P. (2000). Population viability analyses in conservation planning: an overview. *Ecological Bulletins*, *48*, 9–21. https://doi.org/10.2307/20113245

Alberti, M. (2008). Advances in Urban Ecology. In *Advances in Urban Ecology*. Springer. https://doi.org/10.1007/978-0-387-75510-6

Alfeo, A. L., Ferrer, E. C., Carrillo, Y. L., Grignard, A., Pastor, L. A., Sleeper, D. T., Cimino, M. G. C. A., Lepri, B., Vaglini, G., Larson, K., Dorigo, M., & Pentland, A. S. (2019). Urban swarms: A new approach for autonomous waste management. *Proceedings - IEEE International Conference on Robotics and Automation*, *2019-May*, 4233–4240. https://doi.org/10.1109/ICRA.2019.8794020

Alonso, L., Zhang, Y. R., Grignard, A., Noyman, A., Sakai, Y., ElKatsha, M., Doorley, R., & Larson, K. (2018). CityScope: A Data-Driven Interactive Simulation Tool for Urban Design. Use Case Volpe. In A. J. Morales, C. Gershenson, D. Braha, A. A. Minai, & Y. Bar-Yam (Eds.), *Unifying Themes in Complex Systems IX* (pp. 253–261). Springer International Publishing.

Amouroux, E. (2011). *KIMONO , a descriptive agent-based modelling method for the exploration of complex systems : an application to epidemiology .* [Université Pierre et Marie Curie]. https://tel.archives-ouvertes.fr/tel-00630779

Amouroux, E., Desvaux, S., & Drogoul, A. (2008). Towards Virtual Epidemiology: An Agent-Based Approach to the Modeling of H5N1 Propagation and Persistence in North-Vietnam. In T. D. Bui, T. V. Ho, & Q. T. Ha (Eds.), *Intelligent Agents and Multi-Agent Systems* (pp. 26–33). Springer Berlin Heidelberg.

Andersen, M. C. (2005). Potential applications of population viability analysis to risk assessment for invasive species. *Human and Ecological Risk Assessment: An International Journal*, *11*(6), 1083–1095. https://doi.org/10.1080/10807030500278610

Andersen, M. C. (2008). The roles of risk assessment in the control of invasive vertebrates. *Wildlife Research*, *35*(3), 242–248. https://doi.org/10.1071/wr07107

Arias, M., & Sánchez-Vizcaíno, J. M. (2008). African Swine Fever Eradication: The Spanish Model. In *Trends in Emerging Viral Infections of Swine* (pp. 133–139). John Wiley & Sons, Ltd. https://doi.org/10.1002/9780470376812.ch4c

Aronson, M. F. J., La Sorte, F. A., Nilon, C. H., Katti, M., Goddard, M. A., Lepczyk, C. A., Warren, P. S., Williams, N. S. G., Cilliers, S., Clarkson, B., Dobbs, C., Dolan, R., Hedblom, M., Klotz, S., Kooijmans, J. L., Kühn, I., Macgregor-Fors, I., Mcdonnell, M. J., Mörtberg, U., … Winter, M. (2014). A global analysis of the impacts of urbanization on bird and plant diversity reveals key anthropogenic drivers. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1780). https://doi.org/10.1098/rspb.2013.3330

Aronson, M. F. J., Lepczyk, C. A., Evans, K. L., Goddard, M. A., Lerman, S. B., MacIvor, J. S., Nilon, C. H., & Vargo, T. (2017). Biodiversity in the city: key challenges for urban green space management. *Frontiers in Ecology and the Environment*, *15*(4), 189–196. https://doi.org/10.1002/fee.1480

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software, Articles*, *67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01

Baxter, P. W. J., McCarthy, M. a., Possingham, H. P., Menkhorst, P. W., & McLean, N. (2006). Accounting for management costs in sensitivity analyses of matrix population models. *Conservation Biology*, *20*(3), 893–905. https://doi.org/10.1111/j.1523-1739.2006.00378.x

Becker, D. J., Hall, R. J., Forbes, K. M., Plowright, R. K., & Altizer, S. (2018). Anthropogenic resource subsidies and host –parasite dynamics in wildlife. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *373*(1745). https://doi.org/10.1098/rstb.2017.0086

Becker, D. J., Streicker, D. G., & Altizer, S. (2015). Linking anthropogenic resources to wildlife-pathogen dynamics: A review and meta-analysis. *Ecology Letters*, *18*(5), 483–495. https://doi.org/10.1111/ele.12428

Begon, M., Bennet, M., Bowers, R. G., French, N. P., Hazel, S. M., & Turner, J. (2002). A clarification of transmission terms in host-microparasite models: numbers, densities and areas. *Epidemiology and Infection*, *129*(1), 147–153. https://doi.org/10.1017/S0950268802007148

Benton, T. G., & Grant, A. (1999). Elasticity analysis as an important tool in evolutionary and population ecology. *Trends in Ecology and Evolution*, *14*(12), 467–471. https://doi.org/10.1016/S0169-5347(99)01724-3

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*(6), 1203–1213.

Bielby, J., Mace, G. M., Bininda-Emonds, O. R. P., Cardillo, M., Gittleman, J. L., Jones, K. E., Orme, C. D. L., & Purvis, A. (2007). The Fast-Slow Continuum in Mammalian Life History: An Empirical Reevaluation. *The American Naturalist*, *169*(6), 748–757. https://doi.org/10.1086/516847

Blancou, J., Chomel, B. B., Belotto, A., & Meslin, F. X. (2005). Emerging or re-emerging bacterial zoonoses: factors of emergence, surveillance and control. *Veterinary Research*, *3*(5–6), 507–522. https://doi.org/https://doi.org/10.1051/vetres:2005008

Boers, S., Hagoort, K., Scheepers, F., & Helbich, M. (2018). Does residential green and blue space promote recovery in psychotic disorders? A cross-sectional study in the Province of Utrecht, the Netherlands. *International Journal of Environmental Research and Public Health*, *15*(10). https://doi.org/10.3390/ijerph15102195

Boitani, L., Trapanese, P., & Mattei, L. (1985). DEMOGRAPHIC PATTERNS OF A WILD BOAR (Sus scrofa L .) POPULATION IN TUSCANY , ITALY. *Journal of Mountain Ecology*, *3*, 197–201.

Boitani, L., Trapanese, P., & Mattei, L. (1995). Methods of population estimates of a hunted wild boar (Sus scrofa L.) population in Tuscany (Italy). *The Journal of Mountain Ecology*, *3*, 204–208. https://doi.org/10.2981/08-051

Bosch, J., Peris, S., Fonseca, C., Martinez, M., de La Torre, A., Iglesias, I., & Muñoz, M. J. (2012). Distribution, abundance and density of the wild boar on the Iberian Peninsula, based on the CORINE program and hunting statistics. *Folia Zoologica*, *61*(2), 138–151.

Bouwknegt, M., Rutjes, S. A., Reusken, C. B. E. M., Stockhofe-Zurwieden, N., Frankena, K., de Jong, M. C. M., de Roda Husman, A. M., & van der Poel, W. H. M. (2009). The course of hepatitis E virus infection in pigs after contact-infection and intravenous inoculation. *BMC Veterinary Research*, *5*, 1–12. https://doi.org/10.1186/1746-6148-5-7

Braga, C., Alexandre, N., Fernández-Llario, P., & Santos, P. (2010). Wild boar (Sus scrofa) harvesting using the espera hunting method: Side effects and management implications. *European Journal of Wildlife Research*, *56*(3), 465–469. https://doi.org/10.1007/s10344-010-0373-1

Brown, L. R. (2001). Eco-Economy: Building an Economy for the Earth. In Norton (Ed.), *Eco-Economy*. https://doi.org/10.4324/9781315071893

Bui, T. D., Ho, T. V., & Ha, Q. T. (Eds.). (2008). *Intelligent Agents and Multi-Agent Systems* (Vol. 5357). Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-540-89674-6

Burroughs, T., Knobler, S., & Lederberg, J. (2002). The emergence of zoonotic diseases: understanding the impact on animal and human health: workshop summary. In T. Burroughs, S. Knobler, & J. Lederberg (Eds.), *The European Journal of Public Health* (Vol. 14, Issue 2). National Academy Press. https://doi.org/10.1093/eurpub/14.2.219

Cahill, S., & Llimona, F. (2004). Demographics of a wild boar Sus scrofa Linnaeus, 1758 Population in a metropolitan park in Barcelona. *Galemys*, *16*, 37–52.

Cahill, S., Llimona, F., Cabañeros, L., & Calomardo, F. (2012a). 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*(2), 221–233. http://www.scopus.com/inward/record.url?eid=2-s2.0-84871306151&partnerID=40&md5=06fc33d1ceddf697b3913a6aeacc44c7

Cahill, S., Llimona, F., Cabañeros, L., & Calomardo, F. (2012b). What we have learned about wild boar (Sus scrofa) in Collserola Natural Park. *Extended Abstracts of the XXXth IUGB Congress. 5th–9th September.* http://www.iugb2011.com/social/

Cahill, S., Llimona, F., & Gràcia, J. (2003). Spacing and nocturnal activity of wild boar Sus scrofa in a Mediterranean metropolitan park. *Wildlife Biology*, *9*(Artois 1997), 3–13. http://www.parccollserola.net/catalan/actualitat/senglars/CAHILL_SENGLAR.pdf

Campagnolo, E. R., Philipp, L. M., Long, J. M., & Hanshaw, N. L. (2018). Pet-associated Campylobacteriosis: A persisting public health concern. *Zoonoses and Public Health*, *65*(3), 304–311. https://doi.org/10.1111/zph.12389

Carbonero, A., Paniagua, J., Torralbo, A., Arenas-Montes, A., Borge, C., & García-Bocanegra, I. (2014). Campylobacter infection in wild artiodactyl species from southern Spain: Occurrence, risk factors and antimicrobial susceptibility. *Comparative Immunology, Microbiology and Infectious Diseases*, *37*(2), 115–121. https://doi.org/10.1016/j.cimid.2014.01.001

Castillo-Contreras, R. (2019). *Urban wild boar. Drivers of presence, phenotypic responses and health concerns*.

Castillo-Contreras, R., Carvalho, J., Serrano, E., Mentaberre, G., Fernández-aguilar, X., Colom, A., González-Crespo, C., Lavín, S., & López-Olvera, J. R. (2018). Urban wild boars prefer fragmented areas with food resources near natural corridors. *Science of the Total Environment*, *615*, 282–288. https://doi.org/10.1016/j.scitotenv.2017.09.277

Castillo, C. (2019). Wild Boar: A Threat to Europe's Pig Industry. *Modern Concepts & Developments in Agronomy*, *4*(3), 2–5. https://doi.org/10.31031/mcda.2019.04.000586

Choquenot, D., & Ruscoe, W. a. (2003). Landscape complementation and food limitation of large herbivores: Habitat-related constraints on the foraging efficiency of wild pigs. *Journal of Animal Ecology*, *72*(1), 14–26. https://doi.org/10.1046/j.1365-2656.2003.00676.x

Conejero, C., Castillo-Contreras, R., González-Crespo, C., Serrano, E., Mentaberre, G., Lavín, S., & López-Olvera, J. R. (2019). Past experiences drive citizen perception of wild boar in urban areas. *Mammalian Biology*, *96*(April), 68–72. https://doi.org/10.1016/j.mambio.2019.04.002

Conover, M. (2002). *Resolving Wildlife Conflicts*. CRC Press. http://digitalcommons.unl.edu/cgi/viewcontent.cgi?article=1043&context=hwi

Cook, N., & van der Poel, W. H. M. (2015). Survival and Elimination of Hepatitis E Virus: A Review. *Food and Environmental Virology*, *7*(3), 189–194. https://doi.org/10.1007/s12560-015-9196-2

Costanza, R. (1989). Model goodness of fit: A multiple resolution procedure. *Ecological Modelling*, *47*(3–4), 199–215. https://doi.org/10.1016/0304-3800(89)90001-X

Costard, S., Mur, L., Lubroth, J., Sanchez-Vizcaino, J. M., & Pfeiffer, D. U. (2013). Epidemiology of African swine fever virus. *Virus Research*, *173*(1), 191–197. https://doi.org/10.1016/j.virusres.2012.10.030

Costard, S., Wieland, B., de Glanville, W., Jori, F., Rowlands, R., Vosloo, W., Roger, F., Pfeiffer, D. U., & Dixon, L. K. (2009). African swine fever: how can global spread be prevented? *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*(1530), 2683–2696. https://doi.org/10.1098/rstb.2009.0098

Cunningham, A. A. (2005). A walk on the wild side-emerging wildlife diseases. *BMJ*, *331*(7527), 1214–1215. https://doi.org/10.1136/bmj.331.7527.1214

Davis, S., Calvet, E., & Leirs, , H. (2005). Fluctuating Rodent Populations and Risk to Humans from Rodent-Borne Zoonoses. *Vector-Borne and Zoonotic Diseases*, *5*(4), 305–314. https://doi.org/10.1089/vbz.2005.5.305

De la Torre, A., Bosch, J., Iglesias, I., Muñoz, M. J., Mur, L., Martínez-López, B., Martínez, M., & Sánchez-Vizcaíno, J. M. (2015). Assessing the risk of african swine fever introduction into the european union by wild boar. *Transboundary and Emerging Diseases*, *62*(3), 272–279. https://doi.org/10.1111/tbed.12129

DeAngelis, D. L., & Yurek, S. (2017). Spatially Explicit Modeling in Ecology: A Review. *Ecosystems*, *20*(2), 284–300. https://doi.org/10.1007/s10021-016-0066-z

Dearborn, D. C., & Kark, S. (2010). Motivaciones para conservar la biodiversidad urbana. *Conservation Biology*, *24*(2), 432–440. https://doi.org/10.1111/j.1523-1739.2009.01328.x

Decker, D. J., Evensen, D. T. N., Siemer, W. F., Leong, K. M., Riley, S. J., Wild, M. A., Castle, K. T., & Higgins, C. L. (2010). Understanding risk perceptions to enhance communication about human-wildlife interactions and the impacts of zoonotic disease. *ILAR Journal*, *51*(3), 255–261. https://doi.org/10.1093/ilar.51.3.255

Depner, K., Gortazar, C., Guberti, V., Masiulis, M., More, S., Oļševskis, E., Thulke, H., Viltrop, A., Woźniakowski, G., Cortiñas Abrahantes, J., Gogin, A., Verdonck, F., & Dhollander, S. (2017). Epidemiological analyses of African swine fever in the Baltic States and Poland. *EFSA Journal*, *15*(11). https://doi.org/10.2903/j.efsa.2017.5068

Ditchkoff, S. S., Saalfeld, S. T., & Gibson, C. J. (2006). Animal behavior in urban ecosystems: Modifications due to human-induced stress. *Urban Ecosystems*, *9*(1), 5–12. https://doi.org/10.1007/s11252-006-3262-3

Dixon, L. K., Nash, R., Hawes, P. C., & Netherton, C. L. (2019). African Swine Fever Virus. *Reference Module in Life Sciences*. https://doi.org/10.1016/b978-0-12-809633-8.20925-4

Donihue, C. M., & Lambert, M. R. (2015). Adaptive evolution in urban ecosystems. *Ambio*, *44*(3), 194–203. https://doi.org/10.1007/s13280-014-0547-2

Duca, C., Yokomizo, H., Marini, M. a., & Possingham, H. P. (2009). Cost-efficient conservation for the white-banded tanager (Neothraupis fasciata) in the Cerrado, central Brazil. *Biological Conservation*, *142*(3), 563–574. https://doi.org/10.1016/j.biocon.2008.11.010

EFSA. (2014). Scientific Opinion on African swine fever. *EFSA Journal*, *12*(4). https://doi.org/10.2903/j.efsa.2014.3628

Ellis, E. C. (2011). Anthropogenic transformation of the terrestrial biosphere. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences*, *369*(1938), 1010–1035. https://doi.org/10.1098/rsta.2010.0331

Ellis, E. C., & Ramankutty, N. (2008). Putting people in the map: Anthropogenic biomes of the world. *Frontiers in Ecology and the Environment*, *6*(8), 439–447. https://doi.org/10.1890/070062

Ewen, J. G., Walker, L., Canessa, S., & Groombridge, J. J. (n.d.). Improving supplementary feeding in species conservation. *Conservation Biology*, *29*(2), 341–

349. https://doi.org/10.1111/cobi.12410

Fernández-Aguilar, X., Gottschalk, M., Aragon, V., Càmara, J., Ardanuy, C., Velarde, R., Galofré-Milà, N., Castillo-Contreras, R., López-Olvera, J. R., Mentaberre, G., Colom-Cadena, A., Lavín, S., & Cabezón, O. (2018). Urban wild boars and risk for zoonotic streptococcus suis, Spain. *Emerging Infectious Diseases*, *24*(6), 1083–1086. https://doi.org/10.3201/eid2406.171271

Fernández-Llario, P., & Carranza, J. (2000). Reproductive performance of the wild boar in a mediterranean ecosystem under drought conditions. *Ethology Ecology and Evolution*, *12*(4), 335–343. https://doi.org/10.1080/08927014.2000.9522791

Fernández-Llario, P., & Mateos-Quesada, P. (1998). Body size and reproductive parameters in the wild boar Sus scrofa. *Acta Theriologica*, *43*(4), 439–444.

Fernández-Llario, P., & Mateos-Quesada, P. (2005). Influence of rainfall on the breeding biology of Wild boar (Sus scrofa) in a Mediterranean ecosystem. *Folia Zoologica*, *54*(3), 240–248.

Fernández-Martínez, M., Belmonte, J., & Maria Espelta, J. (2012). Masting in oaks: Disentangling the effect of flowering phenology, airborne pollen load and drought. *Acta Oecologica*, *43*, 51–59. https://doi.org/10.1016/j.actao.2012.05.006

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). https://doi.org/10.5751/ES-01560-110106

Focardi, S., Gaillard, J.-M., Ronchi, F., & Rossi, S. (2008). Survival of Wild Boars in a Variable Environment: Unexpected Life-history Variation in an Unusual Ungulate. *Journal of Mammalogy*, *89*(5), 1113–1123. https://doi.org/10.1644/07-MAMM-A-164.1

Focardi, S., Toso, S., & Pecchioli, E. (1996). The population modelling of fallow deer and wild boar in a Mediterranean ecosystem. *Forest Ecology and Management*, *88*(1–2), 7–14. https://doi.org/10.1016/S0378-1127(96)03804-2

Fonseca, C., Santos, P., Monzón, A., Bnto, P., Alves Da Silva, A., Alves, J., Silvério, A., M V M Soares, A., & Petrucci-Fonseca, F. (2004). REPRODUCTION IN THE WILD BOAR (Sus scrofa LINNAEUS , 1758) POPULATIONS OF PORTUGAL. *Galemys*, *16*(nº especial), 53–65. http://dialnet.unirioja.es/servlet/articulo?codigo=1236007&orden=147896&info=link

Gamelon, M., Douhard, M., Baubet, E., Gimenez, O., Brandt, S., & Gaillard, J. M. (2013). Fluctuating fodd resources influence developmental plasticity in wild boar. *Biology Letters*, *9*(5). https://doi.org/10.5061/dryad.8hf1c.2.

Gardner, T. A., Ferreira, J., Barlow, J., Lees, A. C., Parry, L., Vieira, I. C. G., Berenguer, E., Abramovay, R., Aleixo, A., Andretti, C., Aragão, L. E. O. C., Araújo, I., de Ávila, W. S., Bardgett, R. D., Batistella, M., Begotti, R. A., Beldini, T., de Blas, D. E., Braga, R. F., … Zuanon, J. (2013). A social and ecological assessment of tropical land uses at multiple scales: the Sustainable Amazon Network. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *368*(1619), 20120166. https://doi.org/10.1098/rstb.2012.0166

Gavier-Widén, D., Ståhl, K., Neimanis, A. S., Hård Av Segerstad, C., Gortázar, C., Rossi, S., & Kuiken, T. (2015). African swine fever in wild boar in Europe: A notable challenge. *Veterinary Record*, *176*(8), 199–200. https://doi.org/10.1136/vr.h699

Geisser, H., & Reyer, H.-U. (2004). Efficacy of hunting, feeding, and fencing to reduce crop damage by wild boars. *Journal of Wildlife Management*, *68*(4), 939–946. https://doi.org/10.2193/0022-541X(2004)068[0939:EOHFAF]2.0.CO;2

Geisser, H., & Reyer, H.-U. (2005). The influence of food and temperature on population density of wild boar Sus scrofa in the Thurgau (Switzerland). In *Journal of Zoology* (Vol. 267, Issue 01, pp. 89–96). https://doi.org/10.1017/S095283690500734X

Gortázar, C., Ferroglio, E., & Höfle, U. (2007). *Diseases shared between wildlife and livestock : a European perspective*. 241–256. https://doi.org/10.1007/s10344-007-0098-y

Grignard, A., Alonso, L., Taillandier, P., Gaudou, B., Nguyen-Huu, T., Gruel, W., & Larson, K. (2018). The Impact of New Mobility Modes on a City: A Generic Approach Using ABM. In A. J. Morales, C. Gershenson, D. Braha, A. A. Minai, & Y. Bar-Yam (Eds.), *Unifying Themes in Complex Systems IX* (pp. 272–280). Springer International Publishing.

Grimm, N. B., Faeth, S. H., Golubiewski, N. E., Redman, C. L., Wu, J., Bai, X., & Briggs, J. M. (2008). Global change and the ecology of cities. *Science*, *319*(5864), 756–760. https://doi.org/10.1126/science.1150195

Grimm, V. (1999). Ten years of individual-based modelling in ecology: What have we learned and what could we learn in the future? *Ecological Modelling*, *115*(2–3), 129–148. https://doi.org/10.1016/S0304-3800(98)00188-4

Grimm, V., Berger, U., DeAngelis, D. L., Polhill, J. G., Giske, J., & Railsback, S. F. (2010). The ODD protocol: A review and first update. *Ecological Modelling*, *221*(23), 2760–2768. https://doi.org/10.1016/j.ecolmodel.2010.08.019

Guinat, C., Gogin, A., Blome, S., Keil, G., Pollin, R., Pfeiffer, D. U., & Dixon, L. (2016). Transmission routes of African swine fever virus to domestic pigs: Current knowledge and future research directions. *Veterinary Record*, *178*(11), 262–267. https://doi.org/10.1136/vr.103593

Guinat, C., Porphyre, T., Gogin, A., Dixon, L., Pfeiffer, D. U., & Gubbins, S. (2018). Inferring within-herd transmission parameters for African swine fever virus using mortality data from outbreaks in the Russian Federation. *Transboundary and Emerging Diseases*, *65*(2), e264–e271. https://doi.org/10.1111/tbed.12748

Harveson, P. M., Lopez, R. R., Collier, B. A., & Silvy, N. J. (2007). Impacts of urbanization on Florida Key deer behavior and population dynamics. *Biological Conservation*, *134*(3), 321–331. https://doi.org/10.1016/j.biocon.2006.07.022

Hassell, J. M., Begon, M., Ward, M. J., & Fèvre, E. M. (2017). Urbanization and Disease Emergence: Dynamics at the Wildlife–Livestock–Human Interface. *Trends in Ecology and Evolution*, *32*(1), 55–67. https://doi.org/10.1016/j.tree.2016.09.012

Haydon, D. T., Cleaveland, S., Taylor, L. H., & Laurenson, M. K. (2002). Identifying reservoirs of infection: A conceptual and practical challenge. *Emerging Infectious Diseases*, *8*(12), 1468–1473. https://doi.org/10.3201/eid0812.010317

Henry, V. G. (1968). Length of Estrous Cycle and Gestation in European Wild Hogs. In *Source: The Journal of Wildlife Management* (Vol. 32, Issue 2). https://about.jstor.org/terms

Heppel, S. S., Caswell, H., & Crowder, L. B. (2000). Life histories and elasticity patterns : perturbation analysis for species with minimal demographic data. *Ecology*, *81*(3), 654–665.

Heppenstall, A. J. J., Crooks, A. T., See, L. M., & Batty, M. (2012). Agent-based models of geographical systems. In *Agent-Based Models of Geographical Systems*. https://doi.org/10.1007/978-90-481-8927-4

Herr, J., Schley, L., & Roper, T. J. (2009). Socio-spatial organization of urban stone martens. *Journal of Zoology*, *277*(1), 54–62. https://doi.org/10.1111/j.1469-7998.2008.00510.x

Herrera, C. M., Jordano, P., Guitián, J., & Traveset, A. (1998). Annual variability in seed production by woody plants and the masting concept: reassessment of principles and relationship to pollination and seed dispersal. *The American Naturalist*, *152*(4), 576–594. https://doi.org/10.1086/286191

Herrero, J., García-Serrano, A., & García-González, R. (2008). Reproductive and demographic parameters in two Iberian wild boar Sus scrofa populations. *Acta Theriologica*, *53*(4), 355–364. https://doi.org/10.1007/BF03195196

Hobbs, R. J., Arico, S., Aronson, J., Baron, J. S., Cramer, V. A., Epstein, P. R., Ewel, J. J., Klink, C. A., Lugo, A. E., Norton, D., Ojima, D., & Richardson, D. M. (2006).

Novel ecosystems : theoretical and management aspects of the new ecological world order. 1–7. https://doi.org/10.1111/j.1466-822x.2006.00212.x

Hone, J. (2012). Applied Population and Community Ecology: The Case of Feral Pigs in Australia. In *Applied Population and Community Ecology: The Case of Feral Pigs in Australia*. John Wiley & Sons, Ltd. https://doi.org/10.1002/9781118329689

Ikeda, T., Kuninaga, N., Suzuki, T., Ikushima, S., & Suzuki, M. (2019). Tourist-wild boar (Sus scrofa)interactions in urban wildlife management. *Global Ecology and Conservation*, *18*, e00617. https://doi.org/10.1016/j.gecco.2019.e00617

Kansky, R., Kidd, M., & Knight, A. T. (2016). A wildlife tolerance model and case study for understanding human wildlife conflicts. *Biological Conservation*, *201*, 137–145. https://doi.org/10.1016/j.biocon.2016.07.002

Keuling, O., Baubet, E., Duscher, A., Ebert, C., Fischer, C., Monaco, A., Podgórski, T., Prevot, C., Ronnenberg, K., Sodeikat, G., Stier, N., & Thurfjell, H. (2013). Mortality rates of wild boar Sus scrofa L. in central Europe. *European Journal of Wildlife Research*, *59*(6), 805–814. https://doi.org/10.1007/s10344-013-0733-8

Khomenko, S., Beltrán-Alcrudo, D., Rozstalnyy, A., Gogin, A., Kolbasov, D., Pinto, J., Lubroth, J., & Martin, V. (2013). FAO. 2013. African swine fever in the Russian Federation: risk factors for Europe and beyond. EMPRES WATCH, Vol. 28, May 2013. Rome. *EMPRES-LIVESTOCK@fao.Org* |, *28*(May). http://www.jsava.co.zahttp//dx.doi.org/10.4102/jsava.v84i1.1106%0Ahttp://www.jsava.co.za/index.php/jsava/article/view/1106%0Awww.fao.org/ag/empres.html

Koenig, W. D., Knops, J. M. H., Carmen, W. J., & Pearse, I. S. (2015). What drives masting? The phenological synchrony hypothesis. *Ecology*, *96*(1), 184–192. https://doi.org/10.1890/14-0819.1

Kotulski, Y., & Koenig, A. (2008). Conflicts, Crises and Challenges: Wild Boar in the Berlin City - a Social Empirical and Statistical Survey. *Natura Croatica*, *17*(4), 233–246. https://doi.org/york.kotulski@gmx.de

Kowarik, I. (2011). Novel urban ecosystems, biodiversity, and conservation. *Environmental Pollution*, *159*(8–9), 1974–1983. https://doi.org/10.1016/j.envpol.2011.02.022

Kowarik, I. (2018). Urban wilderness: Supply, demand, and access. *Urban Forestry and Urban Greening*, *29*(March 2017), 336–347. https://doi.org/10.1016/j.ufug.2017.05.017

Kuhnert, M., Voinov, A., & Seppelt, R. (2005). Comparing raster map comparison algorithms for spatial modeling and analysis. *Photogrammetric Engineering and Remote Sensing*, *71*(8), 975–984. https://doi.org/10.14358/PERS.71.8.975

Kuijper, D. P. J., Verwijmeren, M., Churski, M., Zbyryt, A., Schmidt, K., Jedrzejewska, B., & Smit, C. (2014). What cues do ungulates use to assess predation risk in dense temperate forests? *PLoS ONE*, *9*(1), 1–12. https://doi.org/10.1371/journal.pone.0084607

Kukielka, D., Rodriguez-Prieto, V., Vicente, J., & Sánchez-Vizcaíno, J. M. (2016). Constant Hepatitis E Virus (HEV) Circulation in Wild Boar and Red Deer in Spain: An Increasing Concern Source of HEV Zoonotic Transmission. *Transboundary and Emerging Diseases*, *63*(5), e360–e368. https://doi.org/10.1111/tbed.12311

Kumar, S., Subhadra, S., Singh, B., & Panda, B. K. (2013). Hepatitis E virus: The current scenario. *International Journal of Infectious Diseases*, *17*(4), e228–e233. https://doi.org/10.1016/j.ijid.2012.11.026

Lacy, R. C. (2005). *Vortex10. A Stochastic Simulation of Extinction Process.*

Lacy, R. C., Miller, P. S., & Traylor-Holzer, K. (2015). *Vortex 10.1 Manual* (Issue April).

Lange, M., & Thulke, H. H. (2017). Elucidating transmission parameters of African swine fever through wild boar carcasses by combining spatio-temporal notification data and agent-based modelling. *Stochastic Environmental Research and Risk Assessment*, *31*(2), 379–391. https://doi.org/10.1007/s00477-016-1358-8

Leong, K. M. (2010). The tragedy of becoming common: Landscape change and perceptions of wildlife. *Society and Natural Resources*, *23*(2), 111–127. https://doi.org/10.1080/08941920802438642

Licoppe, A., Prévot, C., Heymans, M., Bovy, C., Casaer, J., & Cahill, S. (2013). Wild boar / feral pig in (peri-) urban areas. Managing wild boar in human-dominated landscapes. *International Union of Game Biologists - Congress IUGB 2013*, 1–31.

Lischka, S. A., Teel, T. L., Johnson, H. E., Reed, S. E., Breck, S., Don Carlos, A., & Crooks, K. R. (2018). A conceptual model for the integration of social and ecological information to understand human-wildlife interactions. *Biological Conservation*, *225*(December 2017), 80–87. https://doi.org/10.1016/j.biocon.2018.06.020

Llimona, F., Cahill, S., Tenés, A., Camps, D., Bonet-Arbolí, V., & Cabañeros, L. (2007). El estudio de los mamíferos en relación a la gestión de áreas periurbanas. El caso de la región metropolitana de Barcelona. *Galemys*, *19*, 215–234.

Lloyd-smith, J. O., George, D., Pepin, K. M., Pitzer, V. E., Pulliam, J. R. C., Dobson, A. P., Hudson, P. J., & Grenfell, B. T. (2009). Epidemic Dynamics at the Human-Animal Interface. *Science*, *326*(December), 1362–1368.

Lowry, H., Lill, A., & Wong, B. B. M. (2013). Behavioural responses of wildlife to urban environments. *Biological Reviews*, *88*(3), 537–549. https://doi.org/10.1111/brv.12012

Luniak, M. (2004). Synurbization: Adaptation of animal wildlife to urban development.

Proceedings 4th International Urban Wildlife Symposium, 50–55.

Magle, S. B., Hunt, V. M., Vernon, M., & Crooks, K. R. (2012). Urban wildlife research: Past, present, and future. *Biological Conservation*, *155*, 23–32. https://doi.org/10.1016/j.biocon.2012.06.018

Mann, C. C. (2006). *1491: New Revelations of the Americas Before Columbus*. Vintage Books. https://books.google.es/books/about/1491_Second_Edition.html?id=vSCra8jUI2EC&redir_esc=y

Martínez-López, J., Martínez-Fernández, J., Naimi, B., Carreño, M. F., & Esteve, M. A. (2015). An open-source spatio-dynamic wetland model of plant community responses to hydrological pressures. *Ecological Modelling*, *306*(May 2019), 326–333. https://doi.org/10.1016/j.ecolmodel.2014.11.024

Massei, G., & Genov, P. V. (1997). Mortality of wild boar, Sus scrofa, in a Mediterranean area in relation to sex and age. *Journal of Zoology*, *242*(2), 394–400. https://doi.org/10.1111/j.1469-7998.1997.tb05813

Massei, G., & Genov, P. V. (2004). The Environmental Impact of Wild Boar. *Galemys*, *16*, 135–145.

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*(3), 307–320. https://doi.org/10.4098/AT.arch.96-29

Massei, G., Kindberg, J., Licoppe, A., Gačić, D., Šprem, N., Kamler, J., Baubet, E., Hohmann, U., Monaco, A., Ozoliņš, J., Cellina, S., Podgórski, T., Fonseca, C., Markov, N., Pokorny, B., Rosell, C., & Náhlik, A. (2015). Wild boar populations up, numbers of hunters down? A review of trends and implications for Europe. *Pest Management Science*, *71*(4), 492–500. https://doi.org/10.1002/ps.3965

Massei, G., Roy, S., & Bunting, R. (2011). Too many hogs? A review of methods to mitigate impact by wild boar and feralhogs. *Human-Wildlife Interactions*, *5*(1), 79–99.

McCleery, R. A., Moorman, C. E., & Peterson, M. N. (2014). Introduction. In *Urban Wildlife Conservation: Theory and Practice* (pp. 1–10). Springer US. https://doi.org/10.1007/978-1-4899-7500-3_1

Mcdonal, R., Marcotullio, P. J., & Güneralp, B. (2011). Global Effects of Urbanization on Ecosystem Services. In *Urban Ecology* (Vol. 15, Issue 1, pp. 583–605). https://doi.org/10.1093/acprof:oso/9780199563562.003.0024

McDonnell, M. J., & Niemelä, J. (2011). The History of Urban Ecology An Ecologist's Perspective. In *Urban Ecology: Patterns, Processes and Applications* (pp. 5–13). Oxford University Press.

https://doi.org/10.1093/acprof:oso/9780199563562.001.0001

McIntyre, N. E. (2014). Wildlife responses to urbanization: Patterns of diversity and community structure in built environments. In *Urban Wildlife Conservation: Theory and Practice* (pp. 103–115). Springer US. https://doi.org/10.1007/978-1-4899-7500-3_7

McKinney, M. L. (2006). Urbanization as a major cause of biotic homogenization. *Biological Conservation*, *127*(3), 247–260. https://doi.org/10.1016/j.biocon.2005.09.005

McLane, A. J., Semeniuk, C., McDermid, G. J., & Marceau, D. J. (2011). The role of agent-based models in wildlife ecology and management. *Ecological Modelling*, *222*(8), 1544–1556. https://doi.org/10.1016/j.ecolmodel.2011.01.020

McMichael, T. (2004). Review: The emergence of zoonotic diseases: understanding the impact on animal and human health. In *The European Journal of Public Health* (Vol. 14, Issue 2). https://doi.org/10.1093/eurpub/14.2.219

Meng, X. J., Lindsay, D. S., & Sriranganathan, N. (2009). Wild boars as sources for infectious diseases in livestock and humans. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *364*, 2697–2707. https://doi.org/10.1098/rstb.2009.0086

Meslin, F. X. (2008). Public health impact of zoonoses and international approaches for their detection and containment. *Veterinaria Italiana*, *44*(4), 583–590.

Meyerson, F. A. B., Merino, L., & Durand, J. (2007). Migration and environment in the context of globalization. *Frontiers in Ecology and the Environment*, *5*(4), 182–190. https://doi.org/10.1890/1540-9295(2007)5[182:MAEITC]2.0.CO;2

Mills, L. S. (2013). *Conservation of wildlife populations : demography, genetics, and management* (2nd ed.). http://www.lib.ncsu.edu/repository/scholpubs/search?page=detail&cid=71857

Moore, J. E., Corcoran, D., Dooley, J. S. G., Fanning, S., Lucey, B., Matsuda, M., McDowell, D. A., Mégraud, F., Millar, B. C., O'Mahony, R., O'Riordan, L., O'Rourke, M., Rao, J. R., Rooney, P. J., Sails, A., & Whyte, P. (2005). Campylobacter. *Veterinary Research*, *36*(3), 351–382. https://doi.org/10.1051/vetres:2005012

More, S., Miranda, M. A., Bicout, D., Bøtner, A., Butterworth, A., Calistri, P., Edwards, S., Garin-Bastuji, B., Good, M., Michel, V., Raj, M., Nielsen, S. S., Sihvonen, L., Spoolder, H., Stegeman, J. A., Velarde, A., Willeberg, P., Winckler, C., Depner, K., … Gortázar Schmidt, C. (2018). African swine fever in wild boar. *EFSA Journal*, *16*(7). https://doi.org/10.2903/j.efsa.2018.5344

Morelle, K., Podgórski, T., Prévot, C., Keuling, O., Lehaire, F., & Lejeune, P. (2015).

Towards understanding wild boar Sus scrofa movement: A synthetic movement ecology approach. *Mammal Review*, *45*(1), 15–29. https://doi.org/10.1111/mam.12028

Navarro-Gonzalez, N., Castillo-Contreras, R., Casas-Díaz, E., Morellet, N., Concepción Porrero, M., Molina-Vacas, G., Torres, R. T., Fonseca, C., Mentaberre, G., Domínguez, L., Lavín, S., & Serrano, E. (2018). Carriage of antibiotic-resistant bacteria in urban versus rural wild boars. *European Journal of Wildlife Research*, *64*(5). https://doi.org/10.1007/s10344-018-1221-y

Neves, M. I., Malkawi, I., Walker, M., Alaboudi, A., Abu-Basha, E., Blake, D. P., Guitian, J., & Crotta, M. (2019). The transmission dynamics of Campylobacter jejuni among broilers in semi-commercial farms in Jordan. *Epidemiology and Infection*, *147*. https://doi.org/10.1017/S0950268818003308

Newsome, D., & Rodger, K. (2008). To feed or not to feed: A contentious issue in wildlife tourism. *Australian Zoologist*, *34*(SPEC. ISS.), 255–270. https://doi.org/10.7882/fs.2008.029

Niemelä, J., Adams, C. E., & Lindsey, K. J. (2013). Anthropogenic Ecosystems: The Influence of People on Urban Wildlife Populations. In *Urban Ecology* (pp. 116–128). Oxford University Press. https://doi.org/10.1093/acprof:oso/9780199563562.003.0014

Pas, S. D., Man, R. A. De, Mulders, C., Balk, A. H. M. M., Hal, P. T. W. Van, Weimar, W., Koopmans, M. P. G., & Osterhaus, A. D. M. E. (2012). Hepatitis E Virus Infection among Solid Organ Recipients, the Transplant Netherlands. *Emerging Infectious Diseases*, *18*(5), 869–872. https://doi.org/10.3201/eid1805.111712

Patterson, M. E., Montag, J. M., & Williams, D. R. (2003). The urbanization of wildlife management: Social science, conflict, and decision making. *Urban Forestry and Urban Greening*, *1*(3), 171–183. https://doi.org/10.1078/1618-8667-00017

Pavio, N., Meng, X. J., & Doceul, V. (2015). Zoonotic origin of hepatitis e. *Current Opinion in Virology*, *10*. https://doi.org/10.1016/j.coviro.2014.12.006

Pepin, K. M., Davis, A. J., Cunningham, F. L., VerCauteren, K. C., & Eckery, D. C. (2017). Potential effects of incorporating fertility control into typical culling regimes in wild pig populations. *PLoS ONE*, *12*(8), 1–23. https://doi.org/10.1371/journal.pone.0183441

Pérez-Haase, A., & Carreras, J. (2012). *Creació d'una Geobase de dades dels hàbitats CORINE del Parc de Collserola a escala 1:10.000*.

Perez, J., Fernández, A. I., Sierra, M. A., Herráez, P., Fernández, A., & De las Mulas, J. M. (1998). Serological and immunohistochemical study of African swine fever in wild boar in Spain. *Veterinary Record*, *143*(5), 136–139.

https://doi.org/10.1136/vr.143.5.136

Peterson, M. N., Birckhead, J. L., Leong, K., Peterson, M. J., & Peterson, T. R. (2010). Rearticulating the myth of human-wildlife conflict. *Conservation Letters*, *3*(2), 74–82. https://doi.org/10.1111/j.1755-263X.2010.00099.x

Podgórski, T., Apollonio, M., & Keuling, O. (2018). Contact rates in wild boar populations: Implications for disease transmission. *Journal of Wildlife Management*, *82*(6), 1210–1218. https://doi.org/10.1002/jwmg.21480

Podgórski, T., Baś, G., Jędrzejewska, B., Sönnichsen, L., Śnieżko, S., Jędrzejewski, W., Okarma, H., Jędrzejewska, B., Sönnichsen, L., Śnieżko, S., Jędrzejewski, 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*(1), 109–119. https://doi.org/10.1644/12-MAMM-A-038.1

Prange, S., Gehrt, S. D., & Wiggers, E. P. (2004). Influences of anthropogenic resources on raccoon (Procyon, lotor) movements and spatial distribution. *Journal of Mammalogy*, *85*(3), 483–490. https://doi.org/10.1644/BOS-121

Probst, C., Globig, A., Knoll, B., Conraths, F. J., & Depner, K. (2017). Behaviour of free ranging wild boar towards their dead fellows: Potential implications for the transmission of African swine fever. *Royal Society Open Science*, *4*(5). https://doi.org/10.1098/rsos.170054

Rabozzi, G., Bonizzi, L., Crespi, E., Somaruga, C., Sokooti, M., Tabibi, R., Vellere, F., Brambilla, G., & Colosio, C. (2012). Emerging zoonoses: The “one health approach.” *Safety and Health at Work*, *3*(1), 77–83. https://doi.org/10.5491/SHAW.2012.3.1.77

Rakshya, T. (2016). Living with wildlife: Conflict or co-existence. *Acta Ecologica Sinica*, *36*(6), 509–514. https://doi.org/10.1016/j.chnaes.2016.08.004

Riley, S. P. D., Brown, J. L., Sikich, J. A., Schoonmaker, C. M., & Boydston, E. E. (2014). Wildlife friendly roads: The impacts of roads on wildlife in urban areas and potential remedies. In *Urban Wildlife Conservation: Theory and Practice* (pp. 323–360). Springer US. https://doi.org/10.1007/978-1-4899-7500-3_15

Rivero-Juarez, A., Frias, M., Martinez-Peinado, A., Risalde, M. A., Rodriguez-Cano, D., Camacho, A., García-Bocanegra, I., Cuenca-Lopez, F., Gomez-Villamandos, J. C., & Rivero, A. (2017). Familial Hepatitis E Outbreak Linked to Wild Boar Meat Consumption. *Zoonoses and Public Health*, *64*(7), 561–565. https://doi.org/10.1111/zph.12343

Rodewald, A. D., & Gehrt, S. D. (2014). Wildlife population dynamics in urban landscapes. In *Urban Wildlife Conservation: Theory and Practice* (pp. 117–147).

Springer US. https://doi.org/10.1007/978-1-4899-7500-3_8

Rodríguez-Estévez, V., García, A., Perea, J., Mata, C., & Gómez, A. G. (2007). Producción de bellota en la dehesa: factores influyentes. *Arch. Zootec*, *56*, 25–43.

Rosell, C. (1998). Biologia i ecologia del senglar (Sus scrofa L ., 1758) a dues poblacions del nordest ibèric . Aplicació a la gestió. In *Universitat de Barcelona: Vol. Departamen* (Issue PhD). Universitat de Barcelona.

Rosell, C., Fernández-Llario, P., & Herrero, J. (2001). EL JABALÍ (Sus scrofa LINNAEUS, 1758). *Galemys*, *13*(2), 1–25.

Rowlands, R. J., Michaud, V., Heath, L., Hutchings, G., Oura, C., Vosloo, W., Dwarka, R., Onashvili, T., Albina, E., & Dixon, L. K. (2008). African swine fever virus isolate, Georgia, 2007. *Emerging Infectious Diseases*, *14*(12), 1870–1874. https://doi.org/10.3201/eid1412.080591

Ruiz-Fons, F. (2017). A Review of the Current Status of Relevant Zoonotic Pathogens in Wild Swine (Sus scrofa) Populations: Changes Modulating the Risk of Transmission to Humans. *Transboundary and Emerging Diseases*, *64*(1), 68–88. https://doi.org/10.1111/tbed.12369

Salinas, R. A., Stiver, W. H., Corn, J. L., Lenhart, S., Collins, C., Madden, M., Vercauteren, K. C., Schmit, B. B., Kasari, E., Odoi, A., Hickling, G., & Mccallum, H. (2015). An individual-based model for feral hogs in great smoky mountains national park. *Natural Resource Modeling*, *28*(1), 18–36. https://doi.org/10.1111/nrm.12055

Sánchez-Cordón, P. J., Montoya, M., Reis, A. L., & Dixon, L. K. (2018). African swine fever: A re-emerging viral disease threatening the global pig industry. *Veterinary Journal*, *233*(January), 41–48. https://doi.org/10.1016/j.tvjl.2017.12.025

Sánchez-Montoya, M. M., Moleón, M., Sánchez-Zapata, J. A., & Tockner, K. (2016). *Dry riverbeds : corridors for terrestrial vertebrates*. *7*(October), 1–10.

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*(3), 207–212. https://doi.org/10.1007/s10344-005-0025-z

Šatrán, P. (2017). *African swine fever in wild boars in the Czech Republic*. undefined-undefined. https://ec.europa.eu/food/sites/food/files/animals/docs/reg-com_ahw_20171025_african_swine_fever_cze.pdf

Serrano, E., Colom-Cadena, A., Gilot-Fromont, E., Garel, M., Cabezón, O., Velarde, R., Fernández-Sirera, L., Fernández-Aguilar, X., Rosell, R., Lavín, S., & Marco, I. (2015). Border disease virus: An exceptional driver of chamois populations among other threats. *Frontiers in Microbiology*, *6*(DEC), 1–9. https://doi.org/10.3389/fmicb.2015.01307

Servanty, S., Gaillard, J.-M., Ronchi, F., Focardi, S., Baubet, E., & Gimenez, O. (2011). Influence of harvesting pressure on demographic tactics: Implications for wildlife management. *Journal of Applied Ecology*, *48*(4), 835–843. https://doi.org/10.1111/j.1365-2664.2011.02017.x

Servanty, S., Gaillard, J.-M., Toïgo, 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*(6), 1278–1290. https://doi.org/10.1111/j.1365-2656.2009.01579.x

Sih, A., Ferrari, M. C. O., & Harris, D. J. (2011). Evolution and behavioural responses to human-induced rapid environmental change. *Evolutionary Applications*, *4*(2), 367–387. https://doi.org/10.1111/j.1752-4571.2010.00166.x

Spitz, F., & Janeau, G. (1990). Spatial strategies: an attempt to classify daily movements of wild boar. *Acta Theriologica*, *35*(1984), 129–149. https://doi.org/10.4098/at.arch.90-14

Stephens, D. W., & Krebs, J. R. (2020). Foraging Theory. In *Foraging Theory*. Princeton University Press. https://doi.org/10.1515/9780691206790

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*. https://doi.org/10.1111/1365-2664.12756

Stillfried, M., Gras, P., Börner, K., Göritz, F., Painer, J., Röllig, K., Wenzler, M., Hofer, H., Ortmann, S., & Kramer-Schadt, S. (2017). Secrets of success in a landscape of fear: Urban wild boar adjust risk perception and tolerate disturbance. *Frontiers in Ecology and Evolution*, *5*(DEC), 1–12. https://doi.org/10.3389/fevo.2017.00157

Stillfried, M., Gras, P., Busch, M., Borner, K., Kramer-Schadt, S., & Ortmann, S. (2017). Wild inside: Urban wild boar select natural, not anthropogenic food resources. *PLoS ONE*, *12*(4), 1–20. https://doi.org/10.1371/journal.pone.0175127

Strohbach, M. W., Warren, P. S., & Peterson, M. N. (2014). Urban Wildlife Science in Coupled Human--Natural Systems. In R. A. McCleery, C. E. Moorman, & M. N. Peterson (Eds.), *Urban Wildlife conservation: Theory and Practice* (pp. 33–53). Springer US. https://doi.org/10.1007/978-1-4899-7500-3_3

Suselbeek, L., van Wieren, S. E., Jansen, P. A., Bongers, F. J. J. M., & Prins, H. H. T. (2012). Is oak regeneration doomed after wild boar populations boomed? In O. Keuling (Ed.), *Proceedings of the 9th International Symposium on Wild Boar and other Suids* (p. 1).

Swift, B. M. C., Bennett, M., Waller, K., Dodd, C., Murray, A., Gomes, R. L., Humphreys, B., Hobman, J. L., Jones, M. A., Whitlock, S. E., Mitchell, L. J., Lennon, R. J., & Arnold, K. E. (2019). Anthropogenic environmental drivers of antimicrobial resistance in wildlife. *Science of the Total Environment*, *649*, 12–20. https://doi.org/10.1016/j.scitotenv.2018.08.180

Taillandier, P., Gaudou, B., Grignard, A., Huynh, Q. N., Marilleau, N., Caillou, P., Philippon, D., & Drogoul, A. (2019). Building, composing and experimenting complex spatial models with the GAMA platform. *GeoInformatica*, *23*(2), 299–322. https://doi.org/10.1007/s10707-018-00339-6

Tenés, A., Cahill, S., Llimona, F., & Molina, G. (2007). Atropellos de mamíferos y tráfico en la red viaria de un espacio natural en el área metropolitana de Barcelona: quince años de seguimiento en el parque de Collserola. *Galemys*, *19*, 169–188. http://www.researchgate.net/publication/233884168_ATROPELLOS_DE_MAMFEROS_YTRFICO_EN_LA_RED_VIARIA_DE_UN_ESPACIO_NATURAL_EN_EL_REA_METROPOLITANA_DE_BARCELONAQUINCE_AOS_DE_SEGUIMIENTO_EN_EL_PARQUE_DE_COLLSEROLA/file/72e7e51faf6edc72f5.pdf

Toger, M., Benenson, I., Wang, Y., Czamanski, D., & Malkinson, D. (2018). Pigs in space: An agent-based model of wild boar (Sus scrofa) movement into cities. *Landscape and Urban Planning*, *173*(February), 70–80. https://doi.org/10.1016/j.landurbplan.2018.01.006

Toïgo, C., Servanty, S., Gaillard, J.-M., Brandt, S., & Baubet, E. (2008). Disentangling natural from hunting mortality in an intensively hunted wild boar population. *Journal of Wildlife Management*, *72*(7), 1532–1539. https://doi.org/10.2193/2007-378

Torres-Blas, I., Mentaberre, G., Castillo-Contreras, R., Fernández-Aguilar, X., Conejero, C., Valldeperes, M., González-Crespo, C., Colom-Cadena, A., Lavín, S., & López-Olvera, J. R. (2020). Assessing methods to live-capture wild boars (Sus scrofa) in urban and peri-urban environments . *Veterinary Record*, vetrec-2019-105766. https://doi.org/10.1136/vr.105766

Tucker, M. A., Santini, L., Carbone, C., & Mueller, T. (2020). Mammal population densities at a global scale are higher in human-modified areas. *Ecography*, 1–13. https://doi.org/10.1111/ecog.05126

Vetter, S. G., Ruf, T., Bieber, C., & Arnold, W. (2015). What is a mild winter? Regional differences in within-species responses to climate change. *PLoS ONE*, *10*(7), 1–17. https://doi.org/10.1371/journal.pone.0132178

Viana, M., Mancy, R., Biek, R., Cleaveland, S., Cross, P. C., Lloyd-Smith, J. O., &

Haydon, D. T. (2014). Assembling evidence for identifying reservoirs of infection. *Trends in Ecology and Evolution*, *29*(5), 270–279. https://doi.org/10.1016/j.tree.2014.03.002

Virapongse, A., Brooks, S., Metcalf, E. C., Zedalis, M., Gosz, J., Kliskey, A., & Alessa, L. (2016). A social-ecological systems approach for environmental management. *Journal of Environmental Management*, *178*, 83–91. https://doi.org/10.1016/j.jenvman.2016.02.028

Vitousek, P. M., Mooney, H. A., Lubchenco, J., & Melillo, J. M. (2008). Human domination of Earth's ecosystems. *Urban Ecology: An International Perspective on the Interaction Between Humans and Nature*, 3–13. https://doi.org/10.1007/978-0-387-73412-5_1

Vittecoq, M., Godreuil, S., Prugnolle, F., Durand, P., Brazier, L., Renaud, N., Arnal, A., Aberkane, S., Jean-Pierre, H., Gauthier-Clerc, M., Thomas, F., & Renaud, F. (2016). REVIEW: Antimicrobial resistance in wildlife. *Journal of Applied Ecology*, *53*(2), 519–529. https://doi.org/10.1111/1365-2664.12596

Wang, H., Castillo-Contreras, R., Saguti, F., López-Olvera, J. R., Karlsson, M., Mentaberre, G., Lindh, M., Serra-Cobo, J., & Norder, H. (2019). Genetically similar hepatitis E virus strains infect both humans and wild boars in the Barcelona area, Spain, and Sweden. *Transboundary and Emerging Diseases*, *66*(2), 978–985. https://doi.org/10.1111/tbed.13115

Whiley, H., van den Akker, B., Giglio, S., & Bentham, R. (2013). The role of environmental reservoirs in human campylobacteriosis. *International Journal of Environmental Research and Public Health*, *10*(11), 5886–5907. https://doi.org/10.3390/ijerph10115886

Whishaw, I. Q., Hines, D. J., & Wallace, D. G. (2001). Dead reckoning (path integration) requires the hippocampal formation: Evidence from spontaneous exploration and spatial learning tasks in light (allothetic) and dark (idiothetic) tests. *Behavioural Brain Research*, *127*(1–2), 49–69. https://doi.org/10.1016/S0166-4328(01)00359-X

Whittaker, D., Vaske, J. J., & Manfredo, M. J. (2006). Specificity and the cognitive hierarchy: Value orientations and the acceptability of urban wildlife management actions. *Society and Natural Resources*, *19*(6), 515–530. https://doi.org/10.1080/08941920600663912

Worthman, C. M., Plotsky, P. M., Schechter, D. S., & Cummings, C. A. (2010). Formative experiences: The interaction of caregiving, culture, and developmental psychobiology. In *Formative Experiences: The Interaction of Caregiving, Culture, and Developmental Psychobiology*. https://doi.org/10.1017/CBO9780511711879

Xiang, X., Kennedy, R., & Madey, G. (2005). Verification and Validation of Agent-based Scientific Simulation Models. *Agent-Directed Simulation Conference*, 47–55. http://www.nd.edu/~nom/Papers/ADS019_Xiang.pdf

Zhang, B., & DeAngelis, D. L. (2020). An overview of agent-based models in plant biology and ecology. *Annals of Botany*, 1–19. https://doi.org/10.1093/aob/mcaa043

Zhu, Y. G., Reid, B. J., Meharg, A. A., Banwart, S. A., & Fu, B. J. (2017). Optimizing Peri-URban Ecosystems (PURE) to re-couple urban-rural symbiosis. *Science of the Total Environment*, *586*, 1085–1090. https://doi.org/10.1016/j.scitotenv.2017.02.094

Zinsstag, J., Schelling, E., Wyss, K., & Mahamat, M. B. (2005). Potential of cooperation between human and animal health to strengthen health systems. *Lancet*, *366*(9503), 2142–2145. https://doi.org/10.1016/S0140-6736(05)67731-8