

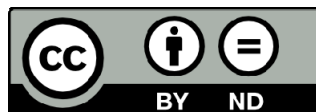


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Wild boar ecology and management in Mediterranean ecosystems

Population dynamics, reproductive ecology
and conflict mitigation

Joana Colomer Rosell



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ecology, and conflict mitigation



JOANA COLOMER ROSELL
DOCTORAL THESIS 2025

Joana Colomer Rosell. Wild boar ecology and management in Mediterranean ecosystems: population dynamics, reproductive ecology and conflict mitigation. Doctoral thesis. Universitat de Barcelona, Barcelona. 2025.

Cover and chapters' cover illustrations: Jose González

Cover design: Joana Colomer & Pep Gaspar (AT comunicació)

Diagrams and schemes: Joana Colomer

This thesis was financially supported by a pre-doctoral grant from Departament d'Innovació, Universitats i Empresa, Generalitat de Catalunya - Pla de Doctorats industrials (2019DI-103)



UNIVERSITAT DE
BARCELONA

Programa de Doctorat en Biodiversitat
Departament Biologia Evolutiva, Ecologia i Ciències Ambientals
Facultat de Biologia

Wild boar ecology and management in Mediterranean ecosystems:

population dynamics, reproductive ecology and conflict mitigation

Ecologia i gestió del senglar en ecosistemes mediterranis:
dinàmiques poblacionals, ecologia reproductiva i mitigació de conflictes

Memòria presentada per
Joana Colomer Rosell
per optar al grau de Doctora per la Universitat de Barcelona
Barcelona 13 de Març 2025

A handwritten signature in black ink, appearing to read "Joana", with a long horizontal stroke extending to the right.

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Per a en Jose.

Acknowledgements (Agraïments)

Al escriure aquestes paraules, me n'adono de la gran quantitat de gent a qui necessito dedicar una frase, i només per això ja em sento molt agraïda!. També he tornat enrere en el moment en que vaig començar la tesi, al 2020, en ple confinament, quan semblava que res tornaria a ser igual i no era clar que es poguessin fer totes les coses que havíem planificat. Però per sort va resultar que si, que poc a poc tot es va posar en marxa i el projecte de doctorat es va poder tirar endavant.

Abans de res, m'agradaria agrair als meus directors de tesi, en Domingo i la Giovanna, que han sabut orientar-me, ajudar-me a millorar i donar-me tot el suport necessari al llarg de tot el doctorat. Sempre mostrant-se a disposició per torbar-nos, xerrar, revisar textos o el que calgués en cada moment. També, m'agradaria agrair a la Carme (en el paper de coautora dels articles publicats), amb qui hem compartit llarguíssimes xerrades sobre la tesi, sobre els resultats, les conclusions i tants altres aspectes, que han enriquit enormement aquesta tesi. Ella va ser la primera que em va despertar el cuquet de fer un doctorat i m'ha donat tota l'energia en les diferents fases. Per això, sense dubtar-ho, puc dir que si no fos per ella tot això no hauria estat possible.

També a tots els companys de minuartia, els quals han anat seguint tot el procés, i especialment a l'Anna, que ha dedicat llargues hores a ajudar-me a entrar i revisar les dades per la tesi, que ho han estat poques!. I a tota la resta de gent amb qui he compartit converses, els companys d'Euroboar i altres investigadors de que treballen amb senglar i que ens anem trobant en simpòsiums, congressos, estades de recerca i que han contribuït també a l'enriquiment d'aquest projecte. També en les diferents persones d'arreu de Catalunya que han contribuït amb la recollida de mostres de senglar, fent anar bidons i mostres amunt i avall.

Al laboratori vaig tenir la companyia inigualable de la Mariàngels, amb la qui la nostra amistat va començar en aquesta mateixa facultat el primer dia de carrera, i hem acabat passant hores i hores al laboratori obrint úters de senglar, comptant cossos luti i pesant fetus.

En general, a tots els meus amics, tant a les que ho sou pràcticament des que vam néixer (Júlia, Isabel i Èrica; gràcies per ser-hi sempre!), com els que ens hem anat trobant després (a la Uni, al CIB, on sigui, que vosaltres ja sabeu qui sou!).

A tots, gràcies per acompanyar-me, tant si viviu al mateix poble, a l'altra punta de Catalunya, o a 4 hores d'avió, us sento sempre molt a prop i trobar-nos per sopar, fer una cervesa, una calçotada, una immersió o pujar alguna muntanya em dona la vida i m'ha permès arribar al final d'aquest procés.

A la meva família, per anar-me preguntant com anava això de la tesi, i donant ànims sobretot a les fases finals per acabar-la de rematar. I en especial als meus pares, Carme i Esteve, gràcies per haver-me fet com soc, per ensenyar-me a estimar la natura, a ser curiosa i constant i per estar al meu costat incondicionalment. Aquest a tesi és també vostra!

Deixo pel final en José, és impossible recollir aquí en dues frases tot el que significa compartir la vida amb tu i poder seguir creixent després de 15 anys junts. Em fas sentir segura i amb força per enfrontar-me a tot, i has estat un suport fonamental per poder fer aquesta tesi i per tota la resta de coses que hem construït junts, i les que queden!

I en definitiva, moltes gràcies a totes aquelles persones que han aportat alguna cosa al llarg d'aquest camí!

Abstract

Wildlife species that exhibit high adaptability and rapid population growth, pose significant challenges for biodiversity management and human-wildlife coexistence. Wild boar (*Sus scrofa*) is an example of such a species, with expanding populations causing increasing conflicts worldwide. Current management approaches are often focused on population control through hunting, but the lack of understanding of the ecological characteristics and responses of this species is limiting their long-term effectiveness. This thesis aims to address the gaps by investigating the ecological mechanisms and drivers behind population dynamics and reproductive strategies, and evaluating the effectiveness of management practices aimed at controlling population growth and mitigating conflict. The research integrates field data collected on wild boar reproduction, camera trap studies, and a long-term dataset of wild boar population density and hunting data from multiple Mediterranean sites. The results identify key factors that influence wild boar density, population growth, and reproductive dynamics. Spring precipitation, forest cover, and female body weight were found to positively influence wild boar density and population growth. Moreover, higher densities lead wild boar populations to experience density-dependent effects, which reduce growth rates and breeding probability. Notably, breeding probability was the only reproductive parameter influenced by density. This suggests that the primary reproductive adjustment to varying population densities is whether or not a female becomes pregnant, rather than the number of offspring produced. The mechanisms through which density affects breeding probability include both indirect effects mediated by body weight and direct effects, potentially mediated by density-dependent changes in behaviour, physiology, social structure or other mechanisms that remain to be fully understood. High densities could be observed in non-hunted areas that are used as refuges during the hunting period. This 'reserve effect' leads to temporarily high densities. The effect provides opportunities for management strategies through occasional population-control driven hunts, which were shown to be effective in long-term reduction of local wild boar numbers, and other strategies such as vaccination campaigns. The findings provide important insights into wild boar ecology, specifically on population dynamics and reproductive strategies in Mediterranean landscapes. They also offer valuable knowledge on how ecological and management factors intersect

to influence species coexistence. As drought conditions are expected to become more frequent and severe in the near future, particularly in Mediterranean areas, reduced water and food availability may naturally limit wild boar population growth. However, these changes may also increase human-wild boar conflicts as this species is increasingly seeking resources in human-dominated landscapes. This highlights the urgent need for integrated, evidence-based management approaches to develop long-term strategies to maintain sustainable population densities and achieve human-wildlife coexistence.

Keywords: Population dynamics, Density-dependence, Reproduction, Wildlife management, *Sus scrofa*

Resum

Les espècies de fauna salvatge amb una gran capacitat d'adaptació i ràpid creixement poblacional suposen un gran repte per a la gestió de la biodiversitat i la coexistència entre humans i fauna. El senglar (*Sus scrofa*) n'és un bon exemple amb poblacions en expansió que generen conflictes creixents a escala global. Els enfocats de gestió actuals es basen sovint en el control poblacional mitjançant la caça, però la manca de coneixement sobre l'ecologia i les respostes d'aquesta espècie en limita l'efectivitat a llarg termini. Aquesta tesi té com a objectiu abordar aquestes llacunes mitjançant l'estudi dels mecanismes ecològics i els factors que determinen la dinàmica poblacional i les estratègies reproductives, així com l'avaluació de l'eficàcia de les mesures de gestió. La recerca integra dades de camp sobre la reproducció del senglar, estudis amb càmeres de fototrampeig i un conjunt de dades de densitat poblacional i caça en diverses localitats mediterrànies. Els resultats identifiquen els factors clau que influeixen en la densitat, el creixement poblacional i la dinàmica reproductiva. S'ha identificat que la precipitació primaveral, la cobertura forestal i el pes de les femelles tenen un efecte positiu sobre la densitat i creixement poblacional del senglar. A més, majors densitats estan associades a menors taxes de creixement poblacional i una menor probabilitat de reproducció. Els mecanismes a través dels quals la densitat afecta la probabilitat de reproducció inclouen tant el pes corporal, com altres factors possiblement relacionats amb canvis en el comportament, la fisiologia, l'estructura social o altres processos encara per aclarir. La probabilitat de reproducció és l'únic paràmetre reproductiu influenciat per la densitat, fet que suggereix que l'ajust principal davant les variacions en la densitat és el fet de si una femella es queda prenyada o no, en comptes d'ajustar la mida de la ventrada. S'ha constatat també que femelles amb més pes presenten una major probabilitat de reproducció i mides de ventrades més grans, confirmant la importància de la condició corporal en l'èxit reproductiu. Per altra banda, s'ha observat un augment de la presència de senglars en àrees no caçades que actuen com a refugis durant el període de caça. Aquest 'efecte reserva', comporta un augment temporal i local de la densitat, que pot oferir oportunitats per a la gestió, com les batudes puntuals de control poblacional, que s'han demostrat efectives en la reducció a llarg termini del nombre d'individus. Els resultats d'aquesta tesis proporcionen informació

clau sobre l'ecologia del senglar i aporten coneixement sobre la interacció entre factors ecològics i de gestió. L'augment previst de les sequeres, especialment a les regions mediterrànies, anirà associat a una reducció de la disponibilitat d'aigua i recursos, que podria limitar de manera natural el creixement poblacional del senglar. No obstant això, aquests canvis també podrien intensificar els conflictes amb els humans, ja que l'espècie buscarà cada cop més recursos en paisatges humanitzats. Això destaca la necessitat d'enfocaments de gestió integrats i basats en evidències per tal de desenvolupar estratègies a llarg termini amb l'objectiu d'assolir densitats de població sostenibles i d'aconseguir la coexistència entre fauna i persones.

Paraules clau: Dinàmica poblacional, Denso-dependència, Reproducció, Gestió de fauna, *Sus scrofa*

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1. General introduction

1.1 Human-wildlife coexistence. A global challenge

Human-wildlife coexistence has become one of the most complex environmental challenges of the twenty-first century. As human populations expand, a paradoxical dynamic has emerged: while many species continue to face severe declines and biodiversity loss remains a critical concern, other species are experiencing significant increases, which often results in environmental and economic impacts. Across Europe and other regions of the world, rewilding processes and rural abandonment have facilitated the recovery of iconic species, such as large carnivores or ungulates, which are expanding their ranges and populations. However, many of these species are increasingly adapting to human-modified landscapes, making it progressively more challenging to achieve human-wildlife coexistence. As rewilding is offering important ecological benefits, it also increases the need for adaptive management to balance the needs of human communities with the species ecological requirements (Butler et al., 2021; Manning et al., 2024; Weber-Hertel & Luther, 2023).

This context implies that interactions of human activity and wildlife have intensified, often resulting in human-wildlife conflicts (HWCs). HWCs occur when the actions of one party negatively affect the other, leading to detrimental consequences for both human communities and wildlife populations (Madden, 2004). Globally, the range of HWCs is broad and includes a variety of issues such as agricultural damage, livestock predation or health risks, among others. These conflicts also pose a conservation threat for some of these species, as they are strongly affected by habitat loss and fragmentation, culling, poaching and other human impacts (Fahrig, 2010; Hilty et al., 2020; Montanheiro Paolino et al., 2024).

The drivers of HWCs are complex and often interconnected, involving ecological, social and economic factors. HWCs typically arise when species adapt to human-modified landscapes, exploiting agricultural resources or urban environments. This phenomenon has been particularly observed in species that are opportunistic feeders or those whose ecological niches overlap with human activities (Frank & Glikman, 2019). Species such as wild boar, wolves, and bears have adapted to these changing environments, leading to increased encounters with humans, which often result in conflict.

Climate change, land-use changes, and the fragmentation of natural habitats have also been identified as significant contributors to human-wildlife conflict (Sillero-Zubiri et al., 2006). Changes in weather patterns and food availability can force species to move out of their natural territories in search of food, water or shelter, which increases their proximity to human settlements. Fast landscape transformation, including rural abandonment, urbanization and agricultural expansion, and infrastructure development have increased these conflicts in both intensity and scale (Dickman, 2010).

Moreover, human dimensions, such as socio-economic factors, cultural attitudes and the perceptions of local communities, play a crucial role in shaping human-wildlife conflict dynamics (Dickman, 2010). Achieving human-wildlife coexistence is critical not only for the well-being of human populations but also for the conservation of biodiversity. Effective conflict mitigation strategies must balance the needs of both wildlife conservation and human livelihoods, integrating ecological research with community engagement and adaptive management approaches (Thapa et al., 2024). In the context of rewilding and escalating challenges posed by human-wildlife conflicts (HWCs), understanding the ecological drivers and mechanisms of wildlife populations is essential for developing adaptive strategies to mitigate negative impacts. The dynamic interplay between human activity and wildlife highlights the necessity of integrating ecological research with proactive management, especially to address the challenges of species that are both ecologically flexible and highly conflictive.

1.2 Wild boar: an example of complex human-wildlife interactions

Unlike large carnivores, which are typically scarce top predators, many ungulate species are considered overabundant, particularly in human-dominated landscapes where predator populations are either extinct or persist at very low densities, and hunting is not allowed. Ungulates often thrive in these predator-free environments, benefiting from reduced predation, low or null hunting pressure and the high availability of anthropogenic resources.

In this context, wild boar (*Sus scrofa*) serves as a paradigmatic example of such ecological dynamics, illustrating the challenges posed by overabundant ungulate populations in anthropogenically altered environments. It is a clear example of the intricate relationship between humans and wildlife. As one of the most widespread large mammals in the world, wild boar is adapted to diverse

ecosystems, ranging from temperate forests to dry Mediterranean environments (Johann et al., 2020). This adaptability, together with the species' high potential for population growth, has significantly increased the overlap between wild boar and human activities, especially in areas with an overabundance or non-sustainable population densities, resulting in more frequent interactions and intensified impacts.

1.2.1 Description of main conflicts and management challenges

Impacts caused by wild boar include, among others, damage to crops, presence in urban areas and risks to public health. These damages often result in significant economic losses, which affect agricultural productivity and the maintenance of public and private infrastructure (Cai et al., 2008; Ficetola et al., 2014; González-Crespo et al., 2018; Ikeda et al., 2019; Schley & Roper, 2003). The main impacts are described below:

- **Damage to crops and pastures:** this is the main source of conflict and leads to substantial economic losses due to compensation and damage mitigation. Wild boars consume a variety of crops, including maize, sunflower, rice, potatoes and grapes in vineyards. In Europe, crops make up 37–88% of their diet (Barrios-Garcia & Ballarí, 2012) and provide high-energy resources that have been linked to larger litter sizes compared to populations feeding in forests (Rosell et al., 2012).
- **Traffic accidents:** wild boar are responsible for a significant number of traffic accidents, accounting for over 80% of wildlife-vehicle collisions in some Mediterranean regions, while their contribution is lower in other areas. But for example, in countries like Sweden saw a 250% increase in wild boar collisions between 2003 and 2011 (Gren et al., 2016).
- **Presence in urban areas:** wild boar incursions into urban areas have increased significantly in many cities (Cahill et al., 2012; Pei et al., 2010). These incursions cause damage to urban infrastructure and pose risks of attacks on humans and potential transmission of zoonotic pathogens.
- **Disease transmission:** wild boar act as vectors for several zoonotic pathogens such as hepatitis E virus (HEV), tuberculosis and antimicrobial-resistant *Campylobacter* (AMR-CAMP), as well as non-zoonotic pathogens such as Classical swine fever and African swine fever (ASF), which has recently emerged in several European countries. (González-Barrio et al., 2015; González-Crespo et al., 2023; Guberti et al., 2019; Rossi et al., 2015; Sáenz-De-Santa-María & Tellería, 2015). The

spread of ASF has dramatic effects on the pig farming industry, leading to the removal of infected animals and restrictions on trade. The economic consequences of these impacts can amount to many millions of euros for the affected countries (Barrios-Garcia & Ballarí, 2012; Guo et al., 2016; Halasa et al., 2016).

- **Impacts on biodiversity:** in areas where wild boar is overabundant, it also poses a threat to biodiversity conservation. Rooting causes disturbances to soil and plant communities, impacts forest regeneration and damages reforestation. Wild boar can also destroy nests and predate on eggs of endangered species (Bongi et al., 2017; Calevo et al., 2017; Carpio et al., 2016; Genov & Massei, 2004; Herrero et al., 2005).

However, wild boar is also considered a keystone species due to its significant role in ecosystem functioning. As active soil diggers and seed dispersers, wild boar contribute to nutrient cycling, vegetation dynamics and soil composition, which helps to support biodiversity and the structure of their habitats (Barrios-Garcia & Ballarí, 2012; Bueno et al., 2009; Genov & Massei, 2004). Moreover, wild boar hunting is a traditional activity and part of the cultural heritage across its native range (Dajczak et al., 2021), with significant ecological and social relevance. In many areas, hunting is the only tool for population control, while also providing economic and recreational value (Apollonio et al., 2010). Furthermore, wild boar may have a role in game meat production, offering an alternative source of protein to farm-raised livestock, which could have environmental benefits by reducing the pressure on traditional agricultural systems.

As a case study, wild boar exemplifies the challenges of managing a species that is ecologically and socially important, but also a source of emerging conflicts that are expected to grow in the context of global change. Effective wild boar management requires balancing their role in ecosystems with the need to mitigate the negative impacts of their interactions with humans and working on the social dimensions to achieve sustainable coexistence.

1.2.2 Key characteristics of wild boar shaping management complexity

Taxonomy and distribution

Wild boar (*Sus scrofa*) is a member of the order Artiodactyla, which includes all even-toed ungulates, and the family Suidae, a group of animals commonly referred to as pigs. The family Suidae consists of several genera, each containing species with distinct morphological and ecological characteristics, including *Sus* (true pigs), *Phacochoerus* (warthogs), *Potamochoerus* (bushpigs), *Hylochoerus* (giant forest hog) and *Babylorosa* (babirusas).

Recent DNA studies confirmed the hypotheses that the Suidae family originated in the islands of Southeast Asia, specifically in Indonesia and the Philippines, and from there spread into mainland Eurasia and North Africa. During this dispersion, a complex speciation event occurred. Molecular phylogenetic studies show that the genus *Sus* diverged from other suids around 10 to 15 million years ago, during the Miocene period. This divergence corresponds with the geographical separation of ancestral suids, which led to the speciation events that produced the diverse genera observed today (Gongora & Moran, 2005). Recent studies provided more information on the phylogenetic structure within the genus *Sus*. Currently, 10 species are recognized, including one classified as extinct. At least four additional species have been proposed by various authors, although their status remains under debate (Box1; Larson et al., 2005; Mona et al., 2007; Olivier, 1993; Wilson & Reeder, 2005).

The wild boar species appeared in Asia around 4 – 4.5 million years ago and the first fossil records is from the Early Pleistocene and dates back to approximately 0.9 – 0.8 million years ago (Ruvinsky et al., 2011; Scandura et al., 2020). When wild boar appeared, it displaced the extinct *S. strozzi*, a large suid likely adapted to swamp environments, which was ancestral to the modern *S. verrucosus* (Kurtén, 1968; Ruvinsky et al., 2011). As *Sus scrofa* expanded its distribution, it experienced a genetic split into western Europe and East Asia genetic lineages that occurred approximately 1.2 million years ago (Frantz et al., 2013; Groenen et al., 2012). This thesis is focused on the European or western wild boar (*Sus scrofa scrofa*).

Box 1. Species of the *Sus* genre accepted in IT IS and Catalogue of Life

Species	Common name	Native distribution	Status IUCN
<i>Sus ahoenobarbus</i>	<i>Palawan Pig</i>	Southern Asia	Vulnerable as <i>S. barbatus ahoenobarbis</i> A separate species from <i>S. barbatus</i> according to Groves (2001b)
<i>Sus barbatus</i>	<i>Bearded pig</i>	Southern Asia	Lower Risk (lc)
<i>Sus bucculentus</i>	Vietnam warty pig	Southern Asia	Listed as Extinct (ex) (Groves, C & Meijaard, 2016)
<i>Sus cebifrons</i>	Visayan warty pig	Southern Asia	Critically Endangered
<i>Sus celebensis</i>	Celebes Warty Pig	Southern Asia	Lower Risk (lc)
<i>Sus oliveri</i>	Oliver's Warty Pig	Southern Asia	Data Deficient A separate species from <i>S. philippensis</i> according to Groves (2001b)
<i>Sus philippensis</i>	Philippine warty pig	Southern Asia	Vulnerable
<i>Sus salvanius</i>	Pygmy Hog	Southern Asia	Critically Endangered
<i>Sus scrofa</i>	Wild boar	Europe & Asia	Lower Risk (lc)
<i>Sus verrucosus</i>	Javan pig	Southern Asia	Endangered

During the Last Glacial Maximum, around 20 thousand years ago, populations declined globally. However, these decreases were more severe in European populations, where wild boar was restricted to relatively small populations in southern regions, from where individuals began expanding their territories after the glacial maximum (Groenen et al., 2012). From the Middle Ages, wild boar suffered a number of anthropogenic influences, until World War II, when populations were significantly reduced or eradicated. They were later replaced with individuals from other regions, either through natural dispersal or human intervention (Apollonio et al., 2010). In addition, wild boar suffered genetic introgression from domestic pigs (*Sus scrofa domesticus*) (Goedbloed et al., 2013; Iacolina et al., 2018, 2019). In southern countries like Italy, Spain and Portugal, there is an extensive overlap between wild boar and domestic pig gene pools. This overlap, which is possibly indicative of long-lasting and frequent

hybridization that is still happening, makes it difficult to evaluate the true genetic and ecological integrity of local populations (De Jong et al., 2023).

Hybridization with domestic pigs not only alters the genetic integrity of wild boar populations, but also the key biological traits. One significant outcome may be the increased reproductive potential, as domestic pigs are selected to produce larger litters and reach sexual maturity earlier. Hybridization can increase reproduction rates in wild boar, accelerating population growth and adding more complexity for species management (Fulgione et al., 2016).

Wild boar is now found on every continent except Antarctica. Within their native range, which includes Asia and Europe, their distribution and population have expanded significantly (Figure 1.1). In recent decades, wild boar has also invaded non-native regions such as the Americas and Australia, where they are classified as invasive species due to their negative impacts on local biodiversity and agriculture ecosystems (Bercê et al., 2021; Glow et al., 2020; USDA, 2024). The global spread of wild boar highlights the challenges of managing their populations, both in their native and invasive ranges.

In Europe, wild boar population densities vary substantially across the continent, influenced by climatic factors, food availability, and human interventions such as hunting and land use changes. Lower densities are observed in northern regions, where harsh climatic conditions restrict survival and reproduction. Higher densities are concentrated in southern and central Europe, where environmental conditions are more favourable. This thesis focuses on wild boar populations in Mediterranean environments, where densities are among the highest in Europe.

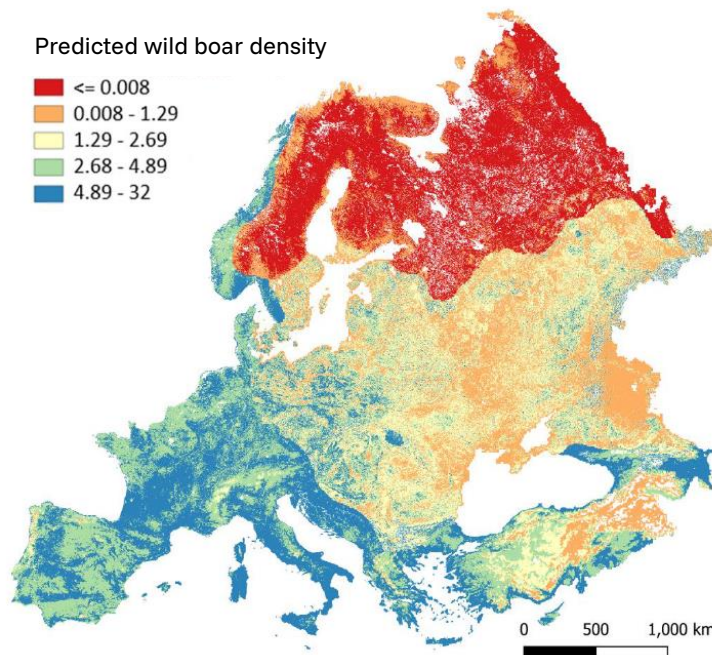


Figure 1.1. Predicted wild boar density (2x2 km resolution) after the calibration of predicted hunting yields-based abundance on a set of reliable density values. Source: ENETWILD-consortium et al., 2024.

Biological and ecological traits

There are several key intrinsic biological and ecological traits of wild boar that make it a very successful species, and at the same time, present significant challenges for its management.

Social structure is based on matriarchal groups, consisting of adult females and their offspring. These groups are typically led by a dominant female, or matriarch. Males, after reaching sexual maturity, generally become solitary except during the rut or mating season, when they seek out females for breeding (Podgórski et al., 2014). This matriarchal social structure supports various cooperative behaviours, including predator avoidance and communal care of the young. It also allows very fast knowledge transmission, which contributes to a group's adaptability to environmental changes and human disturbances (Focardi et al., 2015).

Wild boar **diet characteristics**, as opportunistic omnivores with high flexibility, allow them to use a broad range of food sources. They primarily consume plant material, including roots, tubers, seeds, fruits and agricultural crops, with a strong preference for seasonally abundant resources like acorns and beech mast in autumn and winter. Additionally, they include animal matter in their diet,

such as invertebrates and small vertebrates. Human-related food sources, such as crop waste or supplementary feed, also play a significant role in areas with high human activity (Ballari & Barrios-García, 2014; Giménez-Anaya et al., 2008; Herrero et al., 2003; Schley & Roper, 2003). This adaptability in diet not only supports population growth but also enables wild boar to occupy a variety of habitats. Their ability to exploit diverse food sources makes wild boar highly resilient to specific resource shortages, as they can compensate for the scarcity of one type of food by relying on other available sources.

The reproductive parameters and strategy of wild boar is a key factor in their ecological success. It is characterized by early sexual maturity, large litter sizes and high plasticity, allowing them to quickly adapt to changes in the environment. As reproduction is one of the main topics in this thesis, it is further described in Chapter 1.3.3.

Wild boar **spatial behaviour**, including home range size and daily distances travelled, are highly variable across latitudes, landscapes, seasons and sexes. Males tend to exhibit larger home ranges, with daily movements range from 2 to 10 km (Cavazza et al., 2024) and longer travel distances, which can even increase during the rut, with maximum dispersal distances have been recorded up to 300 km (Popczyk et al., 2024). In contrast, females prioritize energy conservation, often restricting their movements, particularly during periods of high food availability or birthing, with mean daily movements of usually around 5 km/day. Female home ranges have been reported to vary from as little as 200 ha (Fischer et al., 2004; Maillard et al., 1996; Massei et al., 1997a) to as much as 1,600 ha (Gérard & Campan, 1988; Keuling et al., 2008a). These sex-specific strategies reflect the dynamic balance between resource acquisition and reproductive demands (Fattebert et al., 2017; Maillard et al., 1996; Massei et al., 1997a). This high variability also has relevant implications for wildlife managers, as often the administrative limits are smaller than individuals' home ranges and it influences many aspects of management, including disease control strategies, ecological connectivity or measures to mitigate wild boar-vehicle collisions, among others.

Wild boar **activity patterns** are characterized for being predominantly nocturnal with peak activity occurring from dusk until midnight. However, in areas with lower human disturbance, they have been observed to increase their activity during daylight hours (Johann et al., 2020; Keuling et al., 2008b; Rosell et al., 2004; Russo et al., 1997). This behaviour is particularly relevant for conflict mitigation, as dusk and early night are critical periods when most human-wild

boar interactions occur. Therefore, awareness campaigns and mitigation strategies, for example those aimed at reducing wild boar-traffic collisions, should be specifically designed to address these high-risk times of the day.

Therefore, the **high plasticity** of wild boar across various biological and ecological traits is a key factor behind their success as a species. This adaptability enables them to quickly adjust to changing environments, capitalize on available opportunities, and rapidly learn and transmit knowledge. In the context of global change, this plasticity provides them with a competitive advantage, allowing them to expand their range, which increases their overlap with human settlements and leads to dynamic and evolving conflicts.

1.3 Understanding population fluctuations

1.3.1 Population dynamics and density-dependence

Classical population dynamics theories are based on the concept of a fixed carrying capacity (CC), which represents the maximum population size that can be sustained by available resources, such as food and shelter (Lotka, 1932). As a population approaches this capacity, its growth rate slows, eventually stabilizing or fluctuating around this limit. The logistic growth model is an example of this deterministic approach and assumes that environmental conditions and resource availability are relatively stable, with the species responding consistently to changes (Méndez et al., 2015). These assumptions are useful for understanding broad trends in large, stable populations, but fail to account for random events or environmental variability that can significantly impact smaller or more adaptable populations (Kingsland, 1982; Royama, 2021).

In contrast, stochastic population models introduce randomness, which reflects the unpredictability of real-world conditions. The concept of a fixed carrying capacity has been widely discussed, particularly in dynamic ecosystems and species that adapt to fluctuating environments. In such environments, CC is not static but can shift due to changes in resource availability, habitat alteration or human influence (McLeod, 1997). Opportunistic species like wild boar, which are highly adaptable and can cope with diverse and changing conditions, exemplify this argument, as their capacity to adapt to varying habitats makes it almost impossible to define a single, fixed CC (Morellet et al., 2007). Currently, there are multiple statistical approaches for analysing population dynamics under different scopes (Box 2).

In population ecology, density dependence is also a key concept for understanding population dynamics. It refers to regulatory mechanisms through which population size influences various ecological and biological processes. As the population grows, individuals experience greater competition for limited resources, which can have a negative effect on population growth but also behaviour, social structure, reproduction, health or disease dynamics (Bowyer et al., 2014; McCullough, 1999). These processes are typically most pronounced near carrying capacity (CC), when resource limitations and environmental pressures are stronger. However, density dependence can also occur at lower population densities, where limited resources or other environmental pressures may constrain population growth (Mutshinda et al., 2023). While these processes have been well described in many ungulate species, they have not been extensively studied in wild boar populations (Bowyer et al., 2014; Fowler, 1987; Imperio et al., 2012). Density dependence in wild boar populations is often difficult to detect, as it can be masked by the species' high ecological plasticity and ability to adjust demographic traits in response to environmental variability. The species capacity to sustain high densities despite environmental pressures and resource availability complicates the identification of regulatory mechanisms. As a result, population growth is often assumed to be unrestricted by density-dependent factors, and such effects are often overlooked or masked (Bieber & Ruf, 2005; Choquenot, 1998; Servanty et al., 2011).

Krebs (2002) outlines two major paradigms for analysing population dynamics: the density paradigm and the mechanistic paradigm. The density paradigm focuses on the direct relationship between population growth rate and density, and often reveals negative feedback where high densities reduce growth rates. This paradigm provides a broad view of population regulation but often fails in systems where other factors, such as delayed density dependence and stochastic events, can make these relationships difficult to interpret or inconsistent over time (this is the approach in Chapter 1 in this thesis). In contrast, the mechanistic paradigm shifts the focus to specific ecological processes that drive population changes, such as food availability, predation or habitat alteration. This approach highlights the underlying mechanisms that influence population dynamics. In Chapter 2 of this thesis, this paradigm was used to explore the mechanisms of density dependence through reproduction and body condition. These factors and approaches show how complex density

regulation is in shaping population dynamics and how difficult it is to correctly identify its role in wild boar populations. These factors also highlight the importance of considering both density and environmental changes to predict population trends and create effective management strategies.

Box 2. Statistical approaches for population ecology models

A wide range of statistical approaches are available to model population dynamics, each suited for different purposes and requiring distinct types of data. Classical models tend to focus on population growth and regulation, while contemporary models incorporate greater flexibility and stochastic elements to account for uncertainty and variability in ecological systems. Although there are several approaches, the more widely used and accepted are described below:

Models with a classical approach include:

- **Mark-Recapture Models:** Estimates population size, survival rates, and movement patterns based on captured and recaptured individuals. They are used when direct observation of individuals is difficult, especially for elusive species or when studying migratory patterns.
- **Population Viability Analysis (PVA):** Assesses the risk of population extinction over time by incorporating demographic data and environmental variability. PVA is used to inform conservation efforts and evaluate the long-term viability of endangered species under different scenarios.
- **Matrix Population Models:** Track age- or size-structured populations and their transitions between life stages to predict future population size. These models are useful for species with complex life cycles, such as those that go through distinct juvenile, adult, and reproductive stages.
- **Compartmental Models:** Analyse population dynamics in relation to health or disease status, focusing on transitions between compartments like susceptible and infected groups. These models are used in epidemiological studies to understand disease spread and its impact on populations.

Frequent contemporary approaches include:

- **Generalized Linear Models (GLMs):** Extend linear models to handle various data types, such as counts or proportions, by assuming specific distributions. GLMs are widely used in ecological studies where data are not normally distributed, such as count data or binary outcomes.
- **Generalized Additive Models (GAMs):** Model non-linear relationships between population metrics and environmental factors, allowing for flexible data fitting. They are used when the relationship between variables is complex and not easily captured by linear models.
- **Bayesian Inference:** Combines prior knowledge and observed data to estimate population parameters, incorporating uncertainty into the analysis. It is particularly useful in cases with limited data or when prior information from similar studies is available to improve estimates.
- **Individual-Based Models (IBMs):** Simulate individual behaviour and interactions within populations to study complex ecological dynamics. IBMs are used when understanding the behaviour of individuals and their interactions within the population is essential for predicting outcomes, such as studying predator-prey dynamics or the spread of disease.
- **Integrated Population Models (IPMs):** Integrate multiple data sources, such as field surveys, mark-recapture, and genetic data, to provide robust estimates of population size and structure. These models are used when different types of data are available and need to be combined to improve population estimates and address multiple ecological questions.

1.3.2 Population drivers in wild boar

Wildlife populations are regulated by both intrinsic and extrinsic factors (Figure 1.2). Intrinsic factors are biological characteristics of the species that directly affect its population dynamics. These include life-history traits such which are shaped by evolutionary pressures and determine the resilience of a population (Stearns, 1992). Extrinsic factors are external influences on population dynamics, such as environmental conditions, food availability, predation pressure and human interventions (Krebs, 2009).

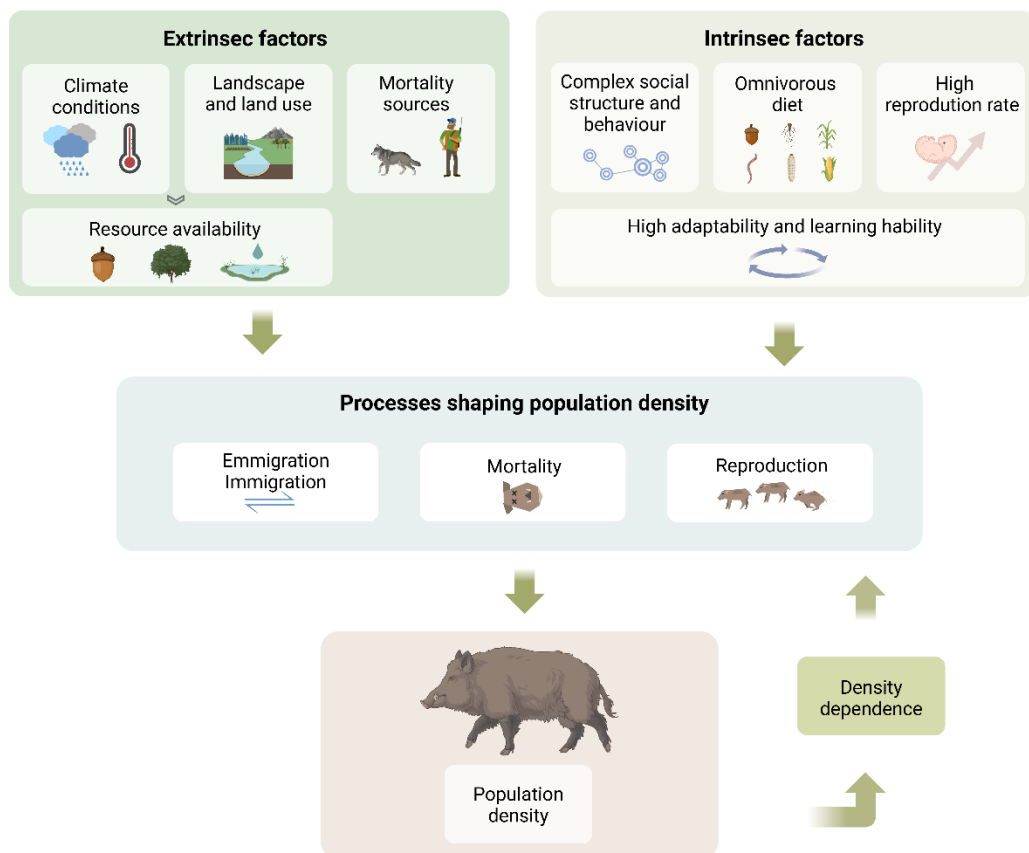


Figure 1.2. Scheme of the extrinsic and intrinsic factors affecting processes that shape wild boar population density. Created in BioRender. Colomer, J. (2025) <https://BioRender.com/a44u614>

Extrinsic factors that influence wild boar populations can be classified in four main types: climate conditions, landscape characteristics, resource availability, and mortality sources.

- **Climate conditions** play a significant role in shaping population dynamics, but the limiting climate factors are highly variable across regions. In northern Europe, mild winters reduce energy demands and improve survival rates, while severe winters increase mortality due to resource scarcity and thermal stress (Borowik et al., 2013; Vetter et al., 2015). In southern areas, precipitation and summer conditions have stronger influences on population growth, mainly through regulating natural resource availability, which ultimately influences survival and reproductive potential (Focardi et al., 2008; Uzal Fernandez & Nores, 2004).
- **Landscape characteristics**, including habitat type and land use, are critical drivers of wild boar population dynamics. Forested areas, the principal habitat for wild boar, have undergone significant changes in many regions due to reforestation programmes, abandonment of agricultural lands, or changes in forestry practices. The expansion of forest cover provides more shelter and abundant natural food sources, which support population growth (Abaigar et al., 1994; Meriggi & Sacchi, 2001). Conversely, deforestation or habitat fragmentation can disrupt populations by reducing the resource availability, which potentially leads to population declines. Agricultural landscapes have created a consistent and abundant food supply, driving population increases in mixed-use areas (Herrero et al., 2006). However, changes in crop type or irrigation system can lead to a fast decrease of resource availability for wild boar and reduce population growth. Urban expansion introduces new challenges, including human-wildlife conflicts, as wild boar increasingly exploit urban green spaces and waste resources (Stillfried et al., 2017).
- **Food availability** is probably the most relevant factor for population dynamics and is highly dependent on climate and landscape characteristics and variations. Specifically, mast production has been widely identified as a strong driver of population fluctuations. Acorn abundance, significantly enhances reproductive success and juvenile survival, leading to population increases in the years following mast-rich

seasons (Bieber & Ruf, 2005; Cutini et al., 2013). Conversely, mast failures result in reduced body condition and lower reproductive rates, often causing declines in population numbers. The availability of anthropogenic resources, such as crops, urban waste and supplementary feeding practices, can further influence wild boar populations by artificially increasing resource availability and buffering against natural food shortages (Keuling et al., 2008b; Stillfried et al., 2017). This increased access to anthropogenic food sources not only increases population growth but also alters wild boar behaviour. For example, it may reduce home range sizes and increase human-wildlife interactions (Herrero et al., 2006; Johann et al., 2020).

- **Mortality sources** also act as regulatory factors in wild boar population dynamics. Adult survival rates are typically over 70%. Overall, hunting is the main cause of mortality in European populations, road accidents, predation and natural mortality have only a small impact (Keuling et al., 2013; Bieber & Ruf, 2005; Fernández-Llario & Carranza, 2000; Melis et al., 2006).

Intrinsic drivers of wild boar population dynamics, such as social structure and behaviour, diet, reproduction rate and high adaptability, are critical to understanding wild boar ecology. These aspects are discussed in-depth in Section 1.2.2, which highlights how the species' characteristics help wild boar to thrive in multiple environments, affecting population dynamics and allowing rapid responses to environmental changes. They can be summed up as:

- **Complex social structure**, organized in matriarchal groups led by dominant females.
- **Behaviour, activity patterns and spatial movement** that are also highly variable and adaptable to changing environmental conditions.
- An **omnivorous and opportunistic diet** allows wild boar to exploit a broad range of food sources.
- Wild boar's **high reproductive rate** and plasticity allows the species to adapt to varying environmental conditions and drives population growth.
- Wild boar exhibits **high adaptability and learning ability**, which enables it to thrive across diverse and changing landscapes, seasons and resource conditions.

These extrinsic and intrinsic factors directly influence key demographic processes that shape population dynamics, such as reproduction, mortality and emigration or immigration. Ultimately, these processes determine population density and long-term trends. By exploring how these drivers interact with one another and respond to environmental changes, we can better anticipate shifts in population size and distribution, which is critical for implementing targeted and sustainable management interventions.

1.3.3 The role of reproduction in wild boar population dynamics

Reproduction is a key driver of wild boar population dynamics, influencing growth rates, density regulation and population structure. Wild boar are an r-strategy species, characterized by early sexual maturity, high reproductive output and rapid population growth. These traits are commonly associated with species that exploit fluctuating or unpredictable environments (Pianka, 1970). Wild boar also exhibit highly flexible reproductive strategies, allowing them to rapidly respond to environmental conditions and resource availability changes. The main characteristics include:

- **Early sexual maturity:** wild boar reach sexual maturity at a remarkably young age, when animals reach a threshold of 30kg approximately, which can occur as early as seven months, depending on environmental conditions and resource availability (Aumaitre et al., 1982; Rosell, 1998). Such precocious reproduction allows wild boar to rapidly increase population size, particularly in favourable conditions, and creates opportunities for quick recovery following population declines due to predation, hunting, or resource shortage in a particular year.
- **Large litter size:** in Central and Northern Europe, litter sizes range from 4.6 to 6.9 piglets (Bieber & Ruf, 2005; Frauendorf et al., 2016; Gethöffer et al., 2007; Náhlik & Sándor, 2003). However, in Mediterranean regions, average litter sizes typically are around 4 piglets per female, with a range between 2.3 and 5.6 (Brogi et al., 2022; Focardi et al., 2008; Massei et al., 1997b; Rosell et al., 2012). This high breeding capability is unusual among large mammals, which generally have smaller litters as a trade-off for larger body size. Both litter size and pregnancy rate are significantly influenced by female body weight. The larger females have the highest reproductive potential, which indicates resource-dependent

fecundity (Aumaitre et al., 1982; Drimaj et al., 2020; Gaillard et al., 1993; Gethöffer et al., 2007; Mauget, 1972).

- **Flexible breeding period:** mating usually takes place during autumn and the beginning of winter, with most conceptions occurring between September and January. Pregnancy lasts for approximately 115 days, and most births occur between February and May (Abaigar, 1992; Mauget, 1972). However, the timing of these events can vary depending on locations and environmental conditions. Some studies found that mating can occur earlier in the year under favourable circumstances, whereas in other locations the pattern is inverted, with favourable years leading to a delay in mating periods (Brogi et al., 2022; Cachelou et al., 2022; Drimaj et al., 2020; Fernández-Llario & Carranza, 2000; Mauget, 1982).
- **Unique metabolic adaptations:** wild boar also presents unusual metabolic adaptations that further support their reproductive strategy. Unlike most large ungulates, which experience peak energy expenditure in early summer, female wild boar reach their highest energy demands earlier in the year, coinciding with key reproductive stages such as gestation and lactation. During summer, their energy metabolism declines, allowing them to conserve resources in preparation for the upcoming rut and mating season. This energy-efficient strategy described in northern populations enhances offspring survival and supports population growth, even under fluctuating environmental conditions (Ruf et al., 2021).

1.4 Current management techniques and strategies

Current management strategies across Europe are diverse (Náhlik et al., 2017) but they often struggle to keep pace with the rapid growth and adaptability of wild boar populations. New policies, such as the European Union's regulations on animal disease control (e.g., EC 2023/594 of 16 March 2023 laying down special disease control measures for African Swine Fever), highlight the need for integrated, evidence-based management approaches, and set an obligation for Member States to establish national action plans for wild boar, which should take account of scientific advice provided by the European Food Safety Authority (EFSA) on preventive measures to reduce and stabilise wild boar density.

- **Hunting** is the main tool available for stabilizing and reducing population sizes and reducing its negative impacts (EFSA et al., 2018). The lack of integration of population ecology principles into management plans limits the ability to design evidence-based strategies for wild boar control. For example, population models that incorporate reproductive rates, survival and dispersal could help managers determine precise harvest quotas and evaluate the potential impacts of management actions. Similarly, predictive tools could identify areas of high population growth or potential conflicts, guiding efforts to optimize resource allocation. Due to the species' high reproductive rate, it has been shown that approximately between 60 and 65% of the population must be harvested annually to achieve effective population control (Croft et al., 2020; Keuling et al., 2013). However, wild boar reproductive rates show high interannual variation depending on climate conditions, food availability and other environmental factors. As a result, culling efforts must be adaptive, aligning with these fluctuations to ensure effective management. This need for flexibility is further complicated by the declining number of hunters across Europe, which poses an increasing challenge to maintaining the efforts to reduce wild boar populations at sustainable levels (Massei et al., 2015). Improving hunting effectiveness and enhancing hunting strategies is indispensable for managing wild boar populations (Frank et al., 2015; Grignolio et al., 2011; Sodeikat & Pohlmeier, 2003; Tolon & Baubet, 2010). Understanding behavioural responses to hunting in specific landscape contexts, such as refuge areas, is essential to select population control and disease management strategies (Keuling & Massei, 2021; Sodeikat & Pohlmeier, 2003; Tolon & Baubet, 2010).
- **Trapping** is also a widely used tool for controlling wild boar populations, particularly in areas where hunting is restricted, such as natural reserves, urban environments or protected areas. This method includes a variety of techniques, such as nets, cage traps or corral traps, among others, which allow for the capture of individuals, providing an effective means to reduce local population densities. However, for a comprehensive and sustainable approach to population management, complementary strategies are still needed to address the broader ecological and demographic challenges.
- **Fertility control** is being actively developed and tested as potential complementary methods for managing wildlife populations. These tools

aim to provide non-lethal alternatives to traditional population control strategies. However, for wild boar a major limitation to their widespread application is the absence of an effective oral contraceptive, which currently prevents the use of fertility control as a complementary tool for population control (Croft et al., 2020; Massei, 2023; Massei & Cowan, 2014).

- **Other individual removal techniques**, such as translocations or the use of toxicants (in countries where wild boar is an invasive alien species) have been used. Translocations are used to remove problematic individuals habituated to urban environments. However, there is no scientific evidence supporting the effectiveness of translocations. This practice is often illegal and not recommended as a realistic and valid solution to solve wild boar overpopulation. The use of toxicants also has considerable drawbacks, as there is a high risk of impact on non-target species and ecosystems and it is not allowed in Europe (Jori et al., 2021)
- **Habitat management** is another key aspect, especially near areas where wild boar presence creates conflicts, such as agricultural lands, infrastructure, urban areas, industrial areas or sensitive natural reserves. One key approach is to limit access to easily obtainable and highly nutritious food sources, such as human rubbish, domestic animals' food or crops, among others, which can significantly attract wild boars and, at the same time, improve their body condition and population growth (Barrios-Garcia & Ballarí, 2012; Castillo-Contreras et al., 2018).
- **Mitigation damage techniques** are employed that include a wide range of measures. Physical barriers, such as fencing, are among the most widely used methods. Electric or mesh fencing can effectively limit access to crops and other sensitive areas, reducing damage and minimizing human-wildlife conflict (Geisser & Reyer, 2004). Deterrents, including acoustic devices, visual stimuli and chemical repellents, are another common approach. These methods aim to scare or discourage wild boar from entering certain areas. Nevertheless, their effectiveness is very limited, and maintenance and reapplication is necessary to reduce wild boar activity in targeted areas (Schlageter & Haag-Wackernagel, 2012). The successful application of these measures requires not only technical adaptation to specific ecological contexts but also significant social involvement (ENETWILD Consortium, 2024).

- **Public awareness and stakeholder engagement** play a crucial role in reducing human-induced factors that worsen wild boar conflicts. The socio-political landscape adds complexity to management efforts. While farmers and landowners often call for aggressive population control to mitigate crop damage, hunters may prefer to maintain high densities for recreational purposes, as hunting is a key part of their cultural and recreational activities. Sometimes their interests (trophy hunt or harvest increase) do not agree with management aims (Keuling et al., 2016; Massei et al., 2015). However, many within the hunting community are aware of the challenges posed by high densities and they play a crucial role in population control efforts. Public administrations increasingly rely on hunters to act as population controllers or wildlife managers, asking them to reduce wild boar densities to mitigate conflicts such as crop damage, road traffic accidents, and disease transmission. At the same time, animal rights associations often oppose lethal control methods, and advocate for non-lethal alternatives (Conejero et al., 2019). Land managers and public authorities must take into account these competing interests and balance recreational hunting, animal welfare concerns, and ecological needs, while ensuring compliance with environmental laws, addressing public safety and assuring human-wild boar coexistence, which is not an easy task. Effective wild boar management strategies must be adapted to specific regional contexts and require continuous monitoring for long-term success (Rosell et al., 2019), which can be achieved using multiple techniques (Box 3). Informed strategies that incorporate ecological knowledge – such as predictive models of population dynamics, spatial distribution and behavioural responses to various control measures – is crucial for designing effective management plans. A data-driven, holistic approach that acknowledges the ecological complexity of wild boar can enhance the sustainability and adaptability of these strategies. Furthermore, research highlights the importance of combining multiple control methods to achieve meaningful population reductions (Massei et al., 2011). Each technique comes with strengths and limitations, which must be carefully weighed depending on the site, objectives and context.

Box 3. Wild boar monitoring techniques

Monitoring wild boar serves multiple purposes, from estimating population size and density to understanding health, reproduction, and movement patterns. As a nocturnal and elusive species, monitoring of wild boar populations has been a challenge for ecologists and wildlife managers (Engeman et al., 2013). There are many methods for density estimation, but often these require a huge amount of resources, making their implementation unfeasible. At large scales, population monitoring has been traditionally based on data provided by different sources:

- **Hunting statistics**, including from basic hunting bags (number of wild boars culled) to more robust and elaborated population density index, which take into account the hunting effort, area of hunting grounds. Data provided by hunters are a valuable source of information that have been showed to provide reliable estimations across time (ENETWILD consortium, 2019; Gamelon et al., 2012). Additionally, reproductive parameters, and other physiological samples derived from harvested individuals offer critical insights into individuals and population dynamics and responses to environmental conditions and management interventions.
- **Field surveys** such as nocturnal transects, faecal counts and snow tracks are also frequent techniques, but in general, they require a huge number of resources in order to obtain robust density estimations.
- **Camera trap images** have emerged as highly useful tool, allowing to obtain robust density estimations through methods such as random encounter model (Massei et al., 2017; Minuartia, 2020; Rowcliffe et al., 2008), and also allow to evaluate ethological parameters, social interactions, group composition, reproductive output, activity patterns and responses to human presence and hunting, among others (Lashley et al., 2018; Oliveira-Santos et al., 2013; Palencia et al., 2019; Rowcliffe et al., 2014, 2016).
- Recently, the use of **drones with thermal cameras** has gained significant attention as an innovative tool for monitoring wild boar populations, assess crop damages or search for carcasses in case of disease outbreak, among others (Kim et al., 2021; Rietz et al., 2023; Rutten et al., 2018).
- Other techniques such as **telemetry data, genetic monitoring or metabolic and physiological monitoring** also provide useful information about the species biology, ecology and response to environmental changes.

1.5 Wild boar populations and their management in Catalonia

The study area of this thesis includes different sites in Catalonia, North-East Spain. In this area, wild boar populations were nearly extinct by the beginning of the twentieth century due to overhunting and habitat loss. However, in recent decades, their numbers have dramatically increased. This increase is primarily attributed to the abandonment of rural areas, changes in forest management practices and land use, the absence of natural predators, and the species' eco-ethological features, which allow them to exploit a wide range of resources, including those from anthropogenic sources (Rosell, 1995).

Currently, populations show varying densities across Catalonia (Figure 1.3). The highest densities are observed in eastern sectors, including Girona and Barcelona provinces, particularly in areas with abundant forest cover, favourable habitats and higher precipitation, where densities can achieve maximums between 15 and 20 wild boar/km². Conversely, in western regions of Catalonia, wild boar populations are less abundant due to less suitable environments. These areas are characterized by more agricultural land, fewer forested areas, drier conditions, and climatic factors such as lower precipitation or more extreme winters in areas such as the Pyrenees, which contribute to lower population densities, typically ranging between 1 and 3 wild boar/km² (DARPA, 2024).

Regarding the reproductive parameters, in the study area, litter size has been reported to range between 3.78 ± 0.27 in different locations for the same year (Rosell, 1998), which is significantly lower than the litter sizes described in northern regions.

In Catalonia, although solitary wolves have been occasionally detected and may establish soon, at present there are no apex predators capable of effectively preying on wild boar. Brown bear is only present in the higher elevations of the Pyrenees and is not a frequent predator of wild boar. As a result, population control relies primarily on hunting. Approximately 70,000 wild boars are harvested each year, which is estimated to represent between 35% and 45% of the total population. The most common and traditional hunting method is driven hunts, or battues, which are widely used across the region. In some areas, particularly where wild boar cause significant damage to agricultural or urban environments, solo hunting at night is occasionally employed. Trapping in urban and peri-urban areas has significantly increased over the past decade due to the

growing presence of wild boar in these areas. It is an important tool for managing wild boar populations in these high-risk areas, particularly in regions where traditional hunting methods may not be feasible or effective. However, data on the number of individuals harvested using these techniques are unavailable.

Supplementary feeding is not permitted in Catalonia, and baiting is strictly regulated. It is only allowed under specific authorizations for damage prevention on crop or livestock, traffic accident prevention or population control. In such cases, the competent authority may authorize the provision of up to 10 kg of food per day (corn, fruit or bread) at a specific location, at least 200 metres away from public roads or paths, and only during the authorized period. This is aimed at attracting animals for trapping purposes. Permanent or automatic feeding systems are prohibited.

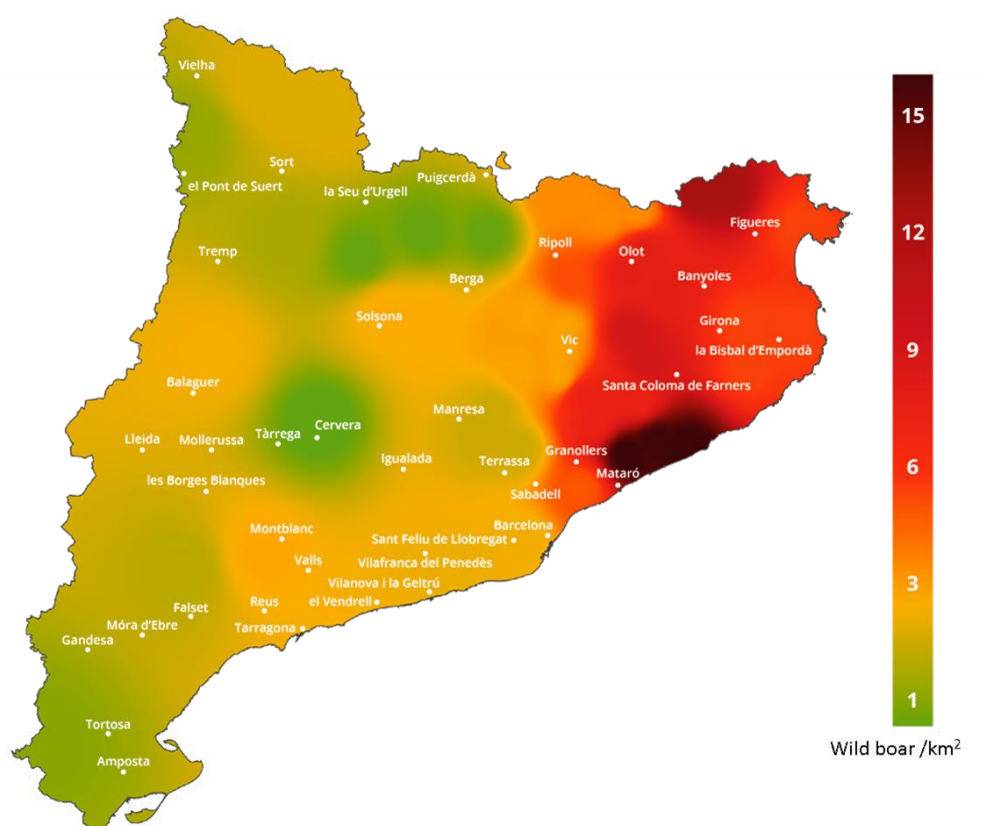


Figure 1.3. Predicted wild boar density (100x100m resolution) extrapolated from densities obtained in the Catalan Wild Boar Monitoring Program. Source: DARP, 2024, available at www.senglar.cat.

1.6 Data sources and study sites

This thesis employs data from multiple sources (Table 1.1): density and population data from the Catalan Wild Boar Monitoring Programme (CWBMP), reproductive tract samples and camera trap images to improve current knowledge on aspects of the wild boar population, with a special focus on improving evidence-based management strategies. Climate and landscape data from various sources have also been used.

Table 1.1. Summary of the data utilized across the different chapters of the thesis, including sources, methodologies, and time periods covered.

Data obtained	Source	Method	Period	Thesis chapter
Climate and landscape data	SMC ¹ and ICGC ²	Climate and land use data analysis	1998-present	1
Density (wild boar/km ²)	CWBMP ³	(Colomer, 2024)	1998-present	1 and 2
Mean male and female weight	CWBMP	Weighting after culling	1998-present	1 and 2
Reproductive parameters and female weight	Reproduction traits collection in this thesis	Uterus and ovaries examination	2021-2023	2
Presence in reserve areas and group composition	Study on reserve areas	Cameratrap data	2013-2016	3

¹Catalan Meteorological Service; ²Cartography and Geology Institute of Catalonia; ³Catalan Wild Boar Monitoring Program

The CWBMP was implemented in 1998, based on previous experiences that started in 1992 in the Zona Volcànica de la Garrotxa Natural Park by the Catalan Government and Barcelona regional council. The monitoring is based on data provided by hunting groups at the end of the seasons. Participants deliver a notebook where data from each driven hunt are recorded including date, number of hunters and dogs, number of wild boars culled, number of wild boars escaped and the place where it was carried out. Currently, more than 173 hunting groups participate in the programme, providing information on about 5,000 hunts each year. The complete database contains data on over 80,000 driven hunts (DARPA, 2024). These data, among other population indicators (such as body weight or sex ratio), can be used to determine a yearly wild boar density value for each of the 23 study sites. The use of hunting data is one of the most widespread methodologies for ungulate density estimation, which allows

the monitoring of large areas with a reasonable economic and time effort. Data provided by hunters are a valuable source of information that has been shown to provide reliable estimations across time (ENETWILD consortium, 2019; Gamelon et al., 2012). Moreover, direct contact with hunting groups and recurrent checks help ensure the data quality. The availability of these long-term series of data from multiple sites, on population density, hunting pressure, and the sex and weight of the individuals hunted, provides an excellent opportunity to expand the knowledge on wild boar population dynamics and its drivers in Mediterranean environments.

For the study of reproductive traits and strategies, an extensive sampling campaign was conducted over three consecutive years to evaluate reproduction outputs. This effort resulted in the collection of 631 female reproductive tract samples from females culled through hunting. These samples were collected with the collaboration of Catalan Government technicians. They contributed by collecting fresh samples right after animals were culled. Samples were preserved and later processed in the laboratory. Sample collection occurred in 10 sites. Nevertheless, from just 5 of these sites a minimum sample size of 20 valid samples/year were obtained, which are the ones included in the analysis. The included sites are representative of different areas in Catalonia, but all of them have a similar habitat dominated by dense forests. Other sites with more varied conditions, such as high-altitude areas in the Pyrenees or drier environments in the south, could not be analysed due the small sample size.

Finally, to research wild boar responses to hunting, especially in reserve areas, camera trap data from three consecutive years were used to assess wild boar presence and group composition before and after population control hunts. The data were collected by colleagues from Minuartia with the support of Montseny Natural Park.



2. Objectives and thesis structure

This thesis aims to increase knowledge about key drivers of the population dynamics and reproduction of wild boar, and to evaluate the 'reserve effect' of non-hunted areas surrounded by hunting grounds and the potential role of these areas to complement population control strategies. By addressing critical knowledge gaps, this project intends to provide a solid scientific foundation to guide decision-making and optimize existing population control and management strategies, particularly in Mediterranean regions.

The specific objectives of the thesis are:

1. Investigate the ecological drivers behind wild boar density and population growth in Mediterranean regions, with a particular emphasis on the role of environmental factors and population characteristics.
2. Examine the role of density dependence and reproductive patterns in wild boar populations, focusing on the possible effect of population density on reproductive success, and the mechanisms behind them.
3. Explore the concept of the 'reserve effect', with a focus on the temporal effects of non-hunted areas on local wild boar densities, and the opportunities these areas provide for managing wild boar populations and mitigating human-wild boar conflicts.

The thesis is structured in three chapters (Figure 2.1):

- **Chapter 1: What drives wild boar density and population growth in Mediterranean environments?** This chapter identifies and analyses the key factors driving wild boar density and population growth in Mediterranean regions, with a focus on objective 1. It examines how climate variables, landscape characteristics and population parameters, such as individuals' weight, sex ratio and density, affect population dynamics. A long-term dataset of wild boar populations from 14 study sites collected for 23 years in Catalonia was used to build two models: one for factors affecting wild boar density and the other for population growth.
- **Chapter 2: Density-dependence and reproductive patterns in Mediterranean wild boar populations.** The second chapter addresses objective 2, which focuses on a deeper understanding of the density dependence patterns identified in Chapter 1 and their effects on wild boar reproductive dynamics. Specifically, it examines associations

between population density – both current and from the previous year – and key reproductive parameters such as litter size, percentage of pregnant females and intrauterine mortality. Additionally, it explores the mechanisms driving these relationships, with particular attention to how density influences reproduction. Moreover, this chapter updates the knowledge of wild boar reproductive parameters in Catalonia, including reproductive timing and fertility parameters that are critical for wildlife management and population control strategies. The study is based on reproductive tracts samples to evaluate reproductive parameters.

- **Chapter 3: 'Reserve effect': An opportunity to mitigate human-wild boar conflicts.** The third chapter focuses on objective 3 and evaluates the 'reserve effect' of a natural reserve area. It assesses whether wild boar moves from areas where hunting occurs to neighbouring sites with no hunting that act as a refuge. As a reserve effect was detected, the chapter also assess the effectiveness of occasional drive hunts inside these reserves on wild boar population control and determines the effects of hunting on wild boar group size and composition. It also examines how these areas can be integrated into management strategies to help control wild boar populations and manage disease outbreaks.

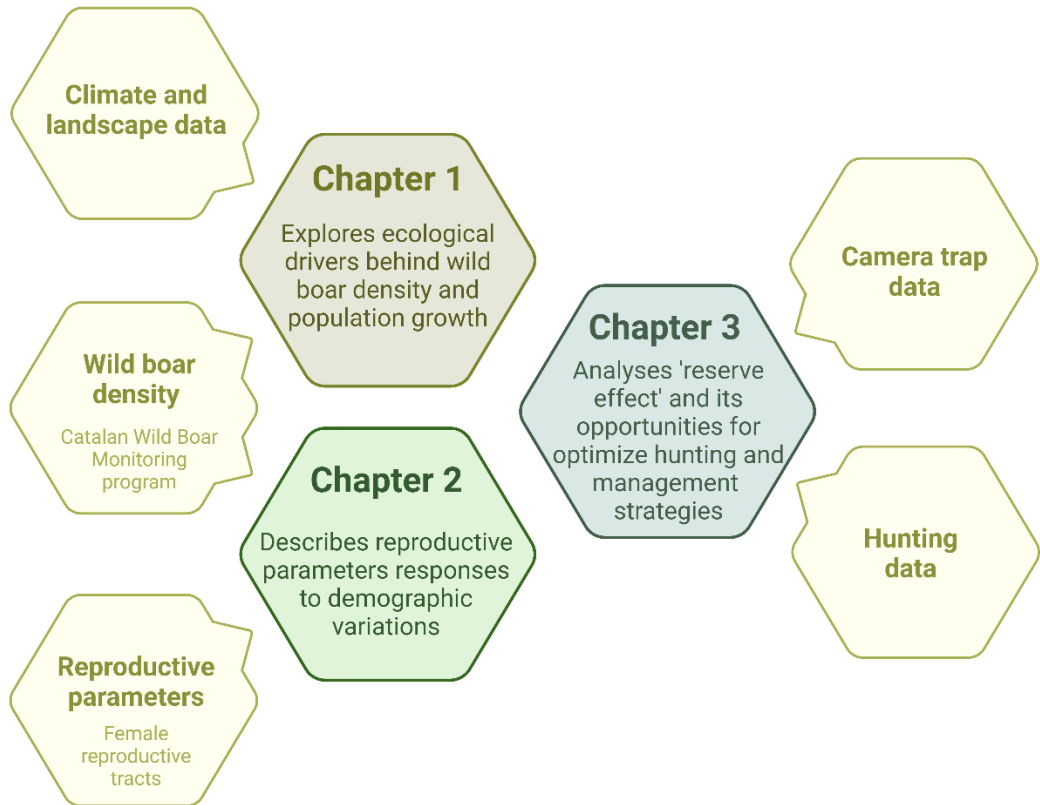
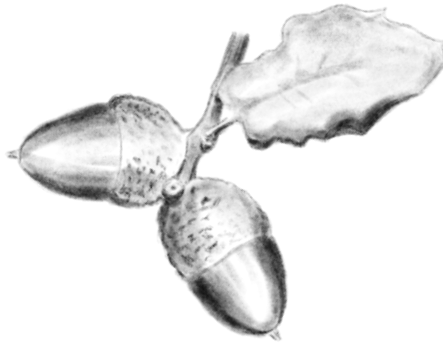


Figure 2.1. Graphical representation of the thesis structure, central hexagons represent the 3 chapters and a short description of the contents. The peripheric hexagons represent data sources used in each chapter.



3. Supervisor's report

Dr. José Domingo Rodríguez Teijeiro and Prof. Giovanna Massei, supervisors of Joana Colomer Rosell's thesis, provide a report on the Impact Factor (IF) of the papers included in his dissertation. The thesis is composed of three different scientific works, of which two are already published in international scientific journals listed in the Science Citation Index (SCI), and the third is under the peer review process. Hereunder, we list the articles, along with the contribution of the candidate to each of them, and the impact factor of each journal. In addition, we certify that no coauthors of these articles or other works presented in this doctoral thesis have used implicitly or explicitly these works as part of other theses.

Chapter 1. Colomer, J., Massei, G., Roos, D., Rosell, C., Rodríguez-Teijeiro, J.D. & 2024. What drives wild boar density and population growth in Mediterranean environments? *Science of the Total Environment*. 931, 172739. DOI: [10.1016/j.scitotenv.2024.172739](https://doi.org/10.1016/j.scitotenv.2024.172739)

Contribution of the candidate: Design and development of analytical methods, interpretation of the results, leading of manuscript writing.

About the journal: *Science of the Total Environment* was evaluated at Journal Citation Reports (JRC) with an Impact Factor of 8,236 (2024). The Impact Factor of the journal was listed as number 31 out of 358 in the field of Environmental sciences (first quartile and first decile).

Chapter 2. Colomer, J., Rodríguez-Teijeiro, J. D., Rosell, C. & Masse, G. Submitted. Evidence of density-dependence in wild boar reproduction. *Biological conservation*

Contribution of the candidate: Coordination of sampling collection, sample processing in laboratory installations, design and development of analytical methods, interpretation of the results, leading of manuscript writing.

About the journal: *Biological conservation* was evaluated at Journal Citation Reports (JRC) with an Impact Factor of 4.952 (2023). The Impact Factor of the journal was listed as number 7 out of 75 in the field of biological conservation (first quartile and second decile) and 25 out of 197 in the field of Ecology (first quartile and second decile).

Chapter 3. Colomer, J., Rosell, C., Rodríguez-Teijeiro, J.D. & Massei, G. 2021. 'Reserve effect': An opportunity to mitigate human-wild boar conflicts. Science of the Total Environment. 795, 148721. [Doi: 10.1016/j.scitotenv.2021.148721](https://doi.org/10.1016/j.scitotenv.2021.148721)

Contribution of the candidate: Design and development of analytical methods, interpretation of the results, leading of manuscript writing.

About the journal: Science of the Total Environment was evaluated at Journal Citation Reports (JRC) with an Impact Factor of 10.753 (2021). The Impact Factor of the journal was listed as number 26 out of 279 in the field of Environmental sciences (first quartile).

Barcelona, March 2025.

A handwritten signature in black ink, appearing to be 'J. Rodríguez-Teijeiro', with a stylized, somewhat abstract form.

Prof. Dr. José Domingo Rodríguez-Teijeiro
Universitat de Barcelona

A handwritten signature in brown ink, appearing to be 'G. Massei', with a cursive, flowing style.

Prof. Dr. Giovanna Massei
University of York



4. Thesis chapters

Chapter 1.

What drives wild boar density and population growth in Mediterranean environments?

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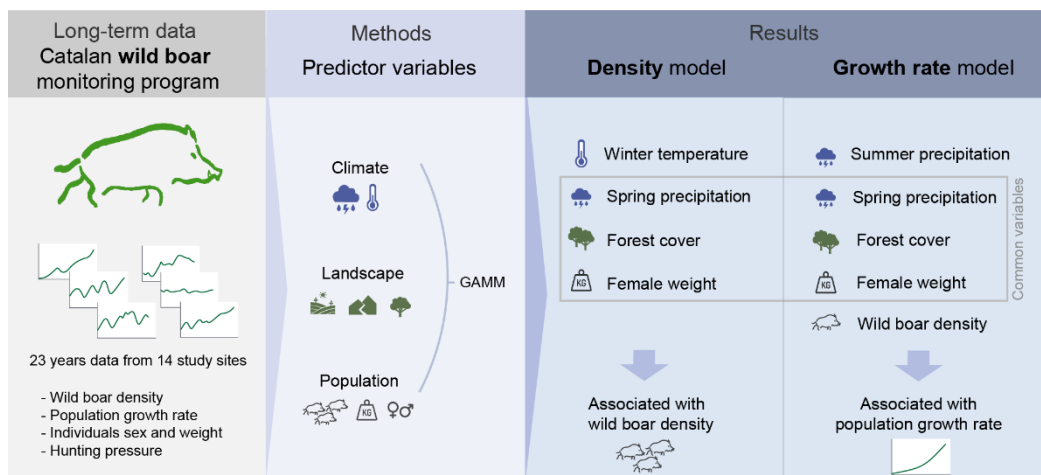
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Published in: Colomer, J., Massei, G., Roos, D., Rosell, C. & Rodríguez-Teijeiro, J.D. 2024. What drives wild boar density and population growth in Mediterranean environments?. *Science of the Total Environment*. 931, 172739. <https://doi.org/10.1016/j.scitotenv.2024.172739>

Highlights

- Effective wildlife management requires accurate predictions of population fluctuations.
- Two models explored factors affecting wild boar density and population growth rate.
- Spring precipitation, forest cover and female weight positively affect wild boar density and population growth.
- Density dependent processes affect wild boar population dynamics.

Graphical abstract



Keywords

Population Dynamics; Environmental factors; Density dependence; Wildlife management; Human-wildlife conflict; *Sus scrofa*

Abstract

Accurate prediction of fluctuations of wildlife local number of individuals is crucial for effective population management to minimise human-wildlife conflicts. Climate, habitat, food availability, and density dependence are among the main factors influencing mammalian population dynamics. In southern Europe, precipitation and temperature, particularly during summer have been suggested as key factors affecting wild boar (*Sus scrofa* L.). However, there is uncertainty regarding the role of these factors and the mechanisms driving population fluctuations. This study utilized long-term data of wild boar populations from 14 study sites collected for 23 years in Catalonia, Spain, to analyse the factors that drive population density and growth rate. Generalized Additive Mixed Models (GAMM) explained respectively, 94% and 65% of the density and growth rate variability. Spring precipitation in both current and previous year, female weight, and forest cover (particularly above 60%) were directly associated with higher wild boar densities and population growth rates. Higher densities were linked to lower population growth in the following year, likely due to a density-dependent process. These findings suggest that the expected decrease in rainfall linked with global warming may limit wild boar population growth. The relationship between climate variables and natural resources availability should be further explored, considering that wild boar can exploit alternative anthropogenic food sources, potentially leading to an increase of human-wildlife conflicts. Therefore, management policies should include measures to limit wild boar access to human-related food, and landscape management measures can also reduce refuge and resource availability in areas with high wild boar impacts. The density-dependence process detected also can have relevant implications for management and we encourage to be further explored.

1 Introduction

Wildlife population dynamics is affected by birth, death, immigration, and emigration, which are in turn influenced by many factors including climate, habitat, food availability, population density and age structure (Krebs, 2002; Moss et al., 1982).

Understanding how these factors influence wild boar (*Sus scrofa* L.) population dynamics is crucial for reliable population forecast and effective management strategies. For instance, the EFSA Panel on Animal Health and Welfare (AHAW) (EFSA et al., 2021) highlighted the need for comprehensive collection and analysis of data on wild boar population dynamics to identify the key demographic drivers associated with this species and improve wild boar management.

The economic impacts of wild boar include crop and infrastructure damage, transmission of diseases to people, livestock and other wildlife, and traffic accidents. Moreover, high densities of wild boar can pose significant threats to biodiversity conservation in sensitive areas (Ballari & Barrios-García, 2014). Generating accurate population dynamics predictions is key to inform decisions about the timing, scale and type of management interventions to prevent or mitigate the negative impacts of this species. This is particularly important in Europe, where wild boar numbers and range have steadily increased in the last decades (Massei et al. 2015).

Compared to other ungulates, wild boar are particularly difficult to manage because of their ecological plasticity and relatively high reproductive rates (Cutini et al., 2013; Fernández-Llario & Carranza, 2000; Fonseca et al., 2011; Giménez-Anaya et al., 2008; Sáez-Royuela & Telleria, 1987). Boar are omnivorous and adapt their diet to locally available resources, with 86%-96% of plant (mostly tree seeds, bulbs and crops) and 10%-20% of animal and fungi matter (Ballari & Barrios-García, 2014; Giménez-Anaya et al., 2008; Herrero et al., 2006; Massei et al., 1996; Schley & Roper, 2003).

Wild boar prefer dense forest habitats, particularly those formed by masting tree species (Abaigar et al., 1994). However, they occur in almost any type of habitat, including agricultural areas, and more recently in urban environments, where

they have access to highly nutritional anthropogenic food (Cahill et al., 2012; Castillo-Contreras et al., 2021; Meriggi & Sacchi, 2001).

Precipitation and temperature, particularly in spring and summer, have been described as key factors affecting wild boar population dynamics in southern Europe. Nevertheless, studies are not unanimous on the role of climate, and factors reported as significant include spring and summer precipitation, (Bisi et al., 2018; Frauendorf et al., 2016), summer temperatures (Focardi et al., 2008; Uzal Fernandez & Nores, 2004) and winter temperatures in colder regions (Borowik et al., 2013).

Climate can impact wild boar dynamics in several ways. For instance, drought can directly affect piglet survival, as piglets have high water requirements during early development (England, 1986; Fernández-Llario & Carranza, 2000; Fraser & Phillips, 1989; Phillips et al., 1990) and dry conditions that harden the soil can make rooting more difficult for all ages, thus reducing food accessibility (Massei et al., 1997).

Weather conditions can also indirectly affect female fecundity. Studies undertaken in Italy and Spain found that spring and summer drought lead to a decrease in the percentage of breeding females (Fernández-Llario & Carranza, 2000; Massei et al., 1996; Sáez-Royuela & Tellería, 1986). Additionally, the effect of climate on the availability of food, such as acorns, affects directly female body weight and litter size (Fonseca et al., 2011; Gamelon et al., 2013; Massei et al., 1996; Mauget, 1972; Rosell et al., 2012). In northern regions (with cooler summers, and barely limited water availability), spring and winter temperatures, snow cover, forest cover and acorn availability appear to have the most pronounced impacts on wild boar dynamics (Borowik et al., 2013; Geisser & Reyer, 2005; Heptner et al., 1988; Jędrzejewska et al., 1997; Melis et al., 2006; Oloff, 1951). Gethöffer et al., 2007, 2023 also showed that precipitation during May and July, together with the number of frost days in February affect wild boar female weight, which is directly related with the reproductive output

Masting events are another factor adding complexity to food availability and wild boar dynamics. Masting events are the highly synchronous production of seeds by various tree species (mostly oak, *Quercus* sp. and beech, *Fagus* sp. in southern Europe) that result in a sudden increase in the availability of high-energy food which directly influence female body weight, especially in forest

habitats (Gethöffer et al., 2023). These resources affect the population dynamics of many ungulate species and of wild boar in particular as this species, unlike other ungulates, is a monogastric and depends on consuming high-energy food for its survival (Barrere et al., 2020; Bieber & Ruf, 2005; Gamelon et al., 2021).

In Mediterranean landscapes the spatial habitat distribution plays a key role for wild boar occurrence (Bosch et al., 2012; Markina-Lamonja, 1998). Wild boar occur more frequently in areas with forest fragments adjacent to large forests and near mountains or riparian woodlands (Giménez-Anaya et al., 2008; Herrero et al., 2006; Virgós, 2002; Acevedo et al., 2006). However, the availability of farmland provides an alternative food source when food is scarce (Abaigar, 1992; Herrero et al., 2006; Sáenz de Buruaga, 1995).

Studies on the effect and extent of density-dependent processes on wild boar population dynamics have reached different conclusions. Some studies suggested that density can influence female body weight, reproductive success and thus population growth (Bruinderink & Hazebroek, 1995; Imperio et al., 2012; Vetter et al., 2015), while other have not found any density-dependence effect on wild boar population growth, fertility or litter size (Choquenot, 1998; Frauendorf et al., 2016; Ditchkoff et al., 2012). Other studies argued that food availability is not regulated by wild boar consumption, as in classic herbivore-plant systems, but it depends on external factors with stochastic variations, hence for this species this density-independent variability would be more prominent than density-dependent processes (Choquenot, 1998; Uzal Fernandez & Nores, 2004)

Most studies on wild boar dynamics have relied on short time series of a single site or on-site comparisons within a single year. However, long-term studies would be ideal for assessing the role of multiple factors on wild boar population dynamics.

The main aim of this study was to investigate the drivers of wild boar demography (population density and growth rate) in 14 sites in a Mediterranean region, where 23 years of wild boar density data are available. This enabled a more robust analysis of wild boar population dynamics with covariates that vary in both time and space and encompass diverse habitats and climate conditions.

Based on the previous studies and knowledge of the populations we formulated four main hypotheses:

1. Wild boar population densities are positively associated with forest cover and habitat diversity.
2. Increased precipitation during spring and summer may lead to higher availability of food resources and survival, resulting in higher population density and growth rate.
3. Female wild boar with higher body weight have better reproductive success, higher survival rates, and higher recruitment rates, leading to higher population density and growth rate.
4. As wild boar densities are still growing, density-dependent processes are unlikely to be a key factor in affecting wild boar population dynamics.

2 Materials and methods

2.1 Study area

The study was conducted in 14 sites spread throughout Catalonia (NE Spain) (Figure 4.1). These sites represent a variety of climatic and habitat typologies in the region (Table 4.1).

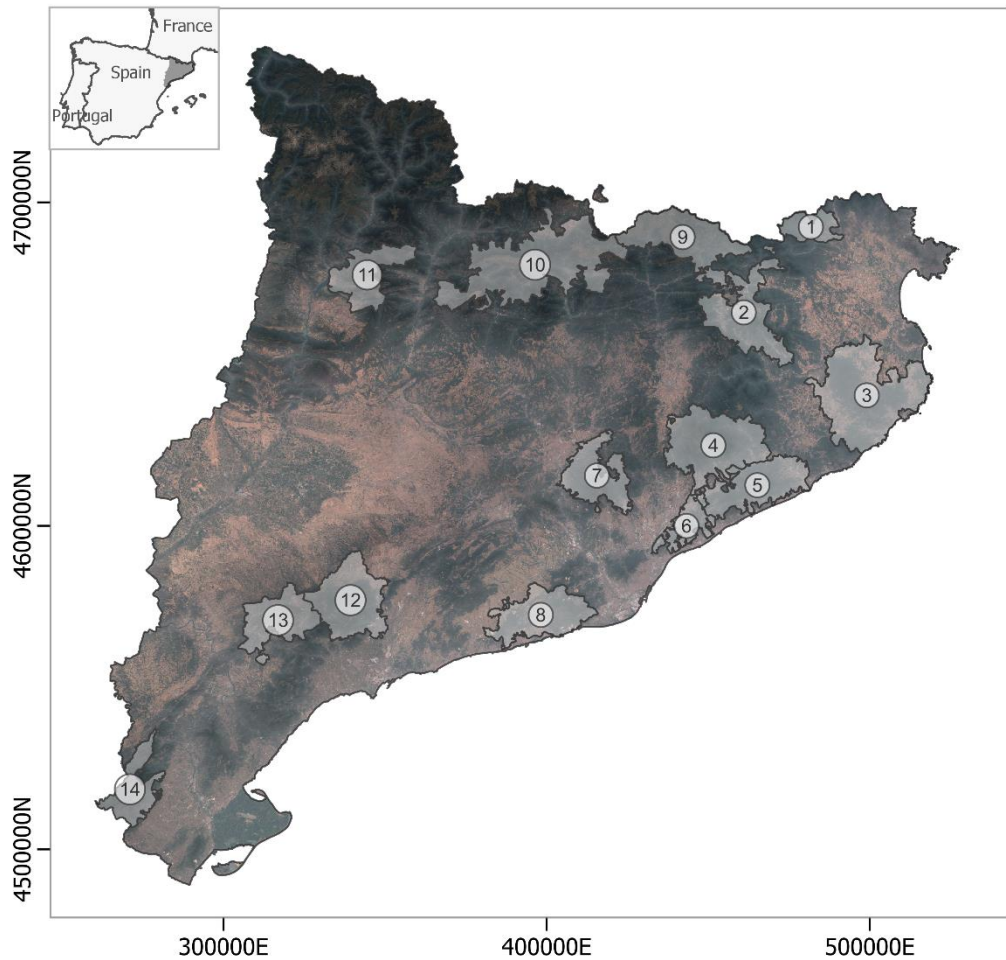


Figure 4.1. Location of the 14 study sites of the Catalan Wild Boar Monitoring Program included in the analysis.

Table 4.1 Characteristics of the 14 study sites included in the analysis. Yearly rainfall and monthly temperatures correspond to the mean of the last 10 years recorded in the nearest meteorological station (data from the Servei Meteorològic de Catalunya).

Sites	Area (ha)	Altitude range (m.a.s.l)	Yearly rainfall (ml)	Mean temp. cooler month (°C)	Mean temp. warmer month (°C)	Wild boar density first monitoring season (wild boar/km ²)	Wild boar density 2021-2022 (wild boar /km ²)
1.Alt Empordà	13.0	53 - 1.451	647.6	7.7	24.0	16.4	17.5
2.Zona Volcànica de la Garrotxa	41.7	136 - 1.513	866.1	5.4	22.7	6.4	15.9
3.Gavarres	70.6	0 - 532	516.5	7.3	24.1	4.5	12.9
4.Montseny	40.7	61 - 1.706	912.8	1.2	20.6	4.1	14.9
5.Montnegre-Corredor	33.6	0 - 760	580.6	8.2	23.9	3.0	15.1
6.Serralades Litoral i de Marina	12.9	11 - 536	581.2	7.5	24.8	3.3	10.5
7.Sant Llorenç del Munt	23.8	148 - 1.103	586.8	6.6	24.0	1.7	7.2
8.Garraf-Olèrdola-Foix	30.2	0 - 657	635.9	7.3	23.7	2.9	5.9
9.Freser-Setcases	21.5	404 - 2.909	1,031.9	2.2	18.9	3.8	6.1
10.Cadí	26.8	603 - 2.648	569.4	0.3	18.4	1.0	2.6
11.Boumort	10.8	501 - 2.077	527,7	2.6	24.7	2.0	4.6
12.Muntanyes de Prades	33.9	118 - 1.200	485.8	6.0	23.4	2.4	5.8
13.Montsant	29.6	79 - 1.163	426.6	5.2	24.6	1.2	4.2
14.Ports de Tortosa i Beseit	28.8	163 - 1.441	648.8	9.4	24.9	1.8	2.2

2.2 Data collection

2.2.1 Wild boar population data

Wild boar population data used in this study were obtained from the Catalan Wild Boar Monitoring Program, which covers 21 study sites across the Catalan territory and began in the 1998-1999 hunting season. Data on wild boar estimated densities were obtained from driven hunts from 1998-1999 to 2020-2021 (23 years) and from 14 sites selected among the 21 sites available. Sites

where data were only available for short periods (< 15 years), or data deemed to have low reliability due to small site area or small number of hunting groups were excluded from analysis. In total there were 290 yearly estimates of wild boar density across 14 sites (Figure 4.2).

Density estimations were derived from hunting bag data from each driven hunt and include date, number of hunters and dogs, number of wild boar culled, and number of animals observed but not culled.

Wild boar density (d) was calculated in the wild boar monitoring program following the method by (Sáez-Royuela & Tellería, 1988), using the equation:

$$d_{i,t} = \frac{\left(\frac{B_{i,t}}{E_{i,t}}\right)}{A_i}$$

where $d_{i,t}$ is the derived density for location i in year t , B is the number of boar hunted, E is the hunting effectiveness ($E_{i,t} = \frac{B_{i,t}}{O_{i,t}}$, where O is the number of boar observed, which includes the hunted and the scaped), and A is the surface area (km²) of the given hunting location.

A total of 290 yearly density estimates were included in the analysis. Density estimates based on hunting bags are often used for monitoring wild boar population trends (Gamelon et al., 2012; Keuling et al., 2018; Massei et al., 2015). The density calculation used in this paper, is also based on hunting bags, but includes a correction for the hunting efficiency (wild boar hunted/wild boar observed). Acevedo et al., 2009 and Segura et al., 2014 showed that hunting effectiveness is highly dependent on local landscape structure parameters and hunters experience among others; thus, correcting for hunting efficiency is key to obtaining more precise population estimates particularly when comparing different areas where the conditions can vary.

Moreover, recent comparison with other density estimation methods based on camera trap, such as the Random Encounter Model (Rowcliffe et al., 2008) carried out in the Montseny natural Park, provided similar density estimates (Minuartia, 2020), strengthening the reliability of the method based on culling and hunting efficiency.

Population growth rate (r_t) was calculated as the log difference in densities of two consecutive years (Roos et al., 2022; Royama, 1992), using the equation:

$$r_{t,i} = \ln(d_{t,i}) - \ln(d_{t-1,i})$$

where $r_{t,i}$ is the proportional growth rate in densities from year $t - 1$ to year t in hunting area i .



Figure 4.2. Wild boar density series for the 14 study sites of the Catalan Wild Boar Monitoring Program included in the analysis. Shadowed in blue are the trends fitted with Generalized Additive Mixed Models with 95% Confidence Intervals for visual aid, the assumptions of the models had not been checked.

2.2.2 Meteorological data

For each of the 14 study sites, meteorological data were obtained from the closest available meteorological station (11 were located within the sites, 2 were within 5 km and the furthest station from a site was 11.6 km). Daily data on precipitation, mean, maximum and minimum temperature, solar radiation and relative humidity were provided by the Catalan Meteorological Service, for the period 01/01/1998 - 31/12/2021. Variables included in the analysis were seasonal, for easier interpretation, with seasons defined as winter (January, February and March); spring (April, May and June); summer (July, August and September) and autumn (October, November and December).

2.2.3 Landscape data

Landscape variables included in the model (Percentage of forest cover and crop cover) were obtained from the land use and cover cartography elaborated by the Cartography and Geology Institute of Catalonia [ICGC] (1987 a 2002) and the Teledetection and Geographical information system research group [Grumets, CREA-UAB] (2007 a 2017)] using the R package 'LandscapeMetrics' (Hesselbarth et al., 2019).

2.3 Conceptual framework

Prior to data analysis, we established a conceptual framework or Directed Acyclic Graph (DAG) (Digitale et al., 2022; Ethier & Nudds, 2017) for an initial consideration of the potential relationship between the different factors affecting wild boar population dynamics. We included in the conceptual framework climate (temperature and precipitation) and landscape factors (such as forest and crop cover, and landscape structure features as altitude, habitat diversity, etc.) that may have an indirect effect mainly through resource availability that in turn may influence population reproduction and mortality. Immigration, emigration, and density dependence processes were also included (Figure 4.3).

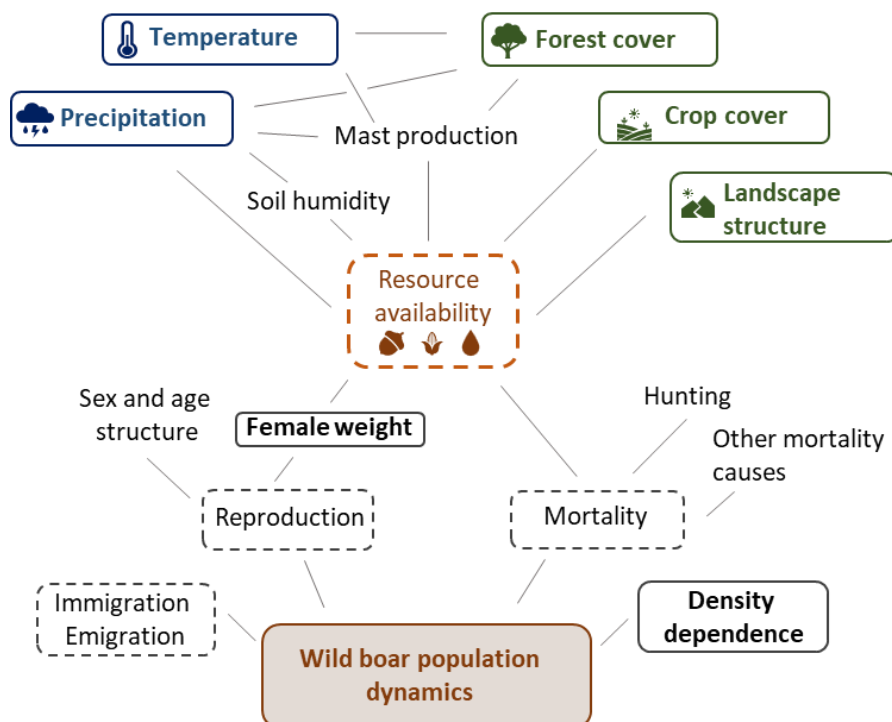


Figure 4.3. Simplified conceptual framework, depicting possible associations of the different drivers of wild boar population dynamics. Bold font indicates factors which we had data for and were included in the analysis.

2.4 Data analysis

Statistical analysis was performed using Generalized Additive Mixed Models (GAMM) to explore the associations of weather conditions, landscape characteristics, and density-dependent processes on wild boar density and population growth rate. A GAMM is a flexible and non-linear regression technique for modelling complex relationships without relying on a predefined functional form, as it allows the estimation both linear and non-linear relationships by using non-parametric smoothing (Murase et al., 2009; Schimek, 2000).

Before running the models, we used Pearson correlation coefficient to measure the linear dependence between two variables. The threshold coefficient was set to ≥ 0.6 but none pair of variables exceeded this value (Zuur et al., 2010).

Two models were run, each using different response variables. The first included derived wild boar population density (wild boar/km²) as the response variable and was modelled as a log-Gaussian distribution (whereby densities were

assumed to be strictly positive). We included weather conditions (seasonal precipitation from current and previous year and temperature from previous year), landscape characteristics (forest cover, crop cover), and population variables (female weight previous year) as fixed effects in the model. The model included both site and year as random effects. The model included the following 15 predictor variables (See Supplementary Materials, Tables S1 and S2): current year winter precipitation ($WP_{i,t}$), previous year winter precipitation ($WP_{i,t-1}$), current year spring precipitation ($SP_{i,t}$), previous year spring precipitation ($SP_{i,t-1}$), previous year autumn precipitation ($AP_{i,t-1}$), current year summer precipitation ($UP_{i,t}$), previous year summer precipitation ($UP_{i,t-1}$), current year total precipitation ($YP_{i,t}$), previous year winter temperature ($WT_{i,t-1}$), previous year spring temperature ($ST_{i,t-1}$), previous year summer temperature ($UT_{i,t-1}$), previous year autumn temperature ($AT_{i,t-1}$), percentage crop surface ($CS_{i,t}$), percentage forest surface ($FS_{i,t}$), previous year female weight ($FW_{i,t-1}$). The model also included 2 random factors (site; $Z_{i,s}$ and year; $Z_{i,y}$) and was based on a sample of 228 observations. Autumn precipitation of the current year was not included as the density is estimated in autumn and there is no time for the autumn precipitation to have any effect. The model was fit using the form:

$$d_{i,t} \sim \text{Normal}(\mu_i, \sigma)$$

$$\log(\mu_i) = \beta_0 + f(WP_{i,t}) + f(SP_{i,t}) + f(UP_{i,t}) + f(WP_{i,t-1}) + f(SP_{i,t-1}) + f(UP_{i,t-1}) + f(AP_{i,t-1}) + f(YP_{i,t}) + f(WT_{i,t-1}) + f(ST_{i,t-1}) + f(UT_{i,t-1}) + f(AT_{i,t-1}) + f(CS_{i,t}) + f(FS_{i,t}) + f(FW_{i,t-1}) + f(YP_{i,t}, CS_{i,t}) + Z_{i,s} + Z_{i,y}$$

In the second model, the response variable was population growth rate ($r_{t,i}$), modelled as a Gaussian distribution. The same variables used in the first model were included in this model, except for wild boar density at time $t - 1$ that was included as a covariate to assess the association with growth rate at time t , to account for 1st order density-dependent processes. The model included 15 predictor variables, 2 random factors (site and year) and was based on a sample of 201 observations. The variables were the same as in the density model except for the inclusion of previous year density and the dropping of yearly precipitation.

Within both GAMMs, for variable selection we included a penalty on the null space of the basis functions (via the 'select=true' argument in the GAMM

function in R) to shrink the terms towards zero, if valid, to prevent overfitting and reduce the complexity of the smooth terms (Marra & Wood, 2011). By setting `select=true` model selection method, we utilized likelihood-based procedures conceptually, similar to variable selection with Akaike Information Criterion (AIC) and the Bayesian Information Criterion (BIC) to identify the most suitable model that balances goodness of fit with model complexity. This model selection process is essential for ensuring that the chosen GLMM accurately captures the relationships within the data, particularly in the context of ecological research where the selection of predictors is a critical aspect of model development. Relevant variables were selected through visual inspection of the smooth plots, further enhancing the model's validity and interpretability. Model assumptions, such as overdispersion and residual plots, were checked to ensure the validity of the model. For both models assumptions were considered to be met (see Supplementary materials, Figure S1 and Figure S2). Restricted Maximum Likelihood (REML) was used to estimate the variance components in the mixed model, ensuring unbiased estimates of the parameters. Cubic regression splines were used for constructing smooth terms. Maximum number of knots were set to 10. To assess autocorrelation of population growth rate, we employed the autocorrelation function (ACF). In our analysis, no significant autocorrelation in the ACF plot (Supplementary materials Figure S3) was detected, indicating that the population growth at a given time point is not strongly correlated with its immediate historical values. All GAMM analyses were carried out in R 4.51.1 (R Core Team, 2022) 'mgcv' version 1.8-33 (Wood, 2023).

3 Results

The wild boar density GAMM model had a good fit with the data, with 94.1% of the deviance explained. Spring precipitation and previous year spring precipitation had both a clear positive, linear effect on wild boar density, with higher wild boar densities associated with higher precipitation during the spring months (March, April and May) of current and previous year. Mean winter temperature of previous year had a significant non-linear effect, with a positive effect until a threshold around 7°C; beyond this, the effect transitions into a slightly negative trend. Mean female weight of the previous year showed a significant positive effect, with a stronger effect at the lower weight range, from 33 to 43 kg. The percentage of forest cover also showed a significant association, with a notable positive relationship above 60% of forest cover (Figure 4.4, and supplementary materials Figure S4).

The population growth GAMM model had a lower fit with the data, with 65.8% of the deviance explained. The four variables significant for the density model (spring precipitation, previous year spring precipitation, previous year female weight and forest cover), were also significant in the growth model, with similar patterns. Moreover, density had a significant negative effect and previous year summer precipitation was also found as a relevant factor with a non-linear effect with a positive trend above 200 mm of total rainfall (Figure 4.5, and supplementary materials Figure S5).

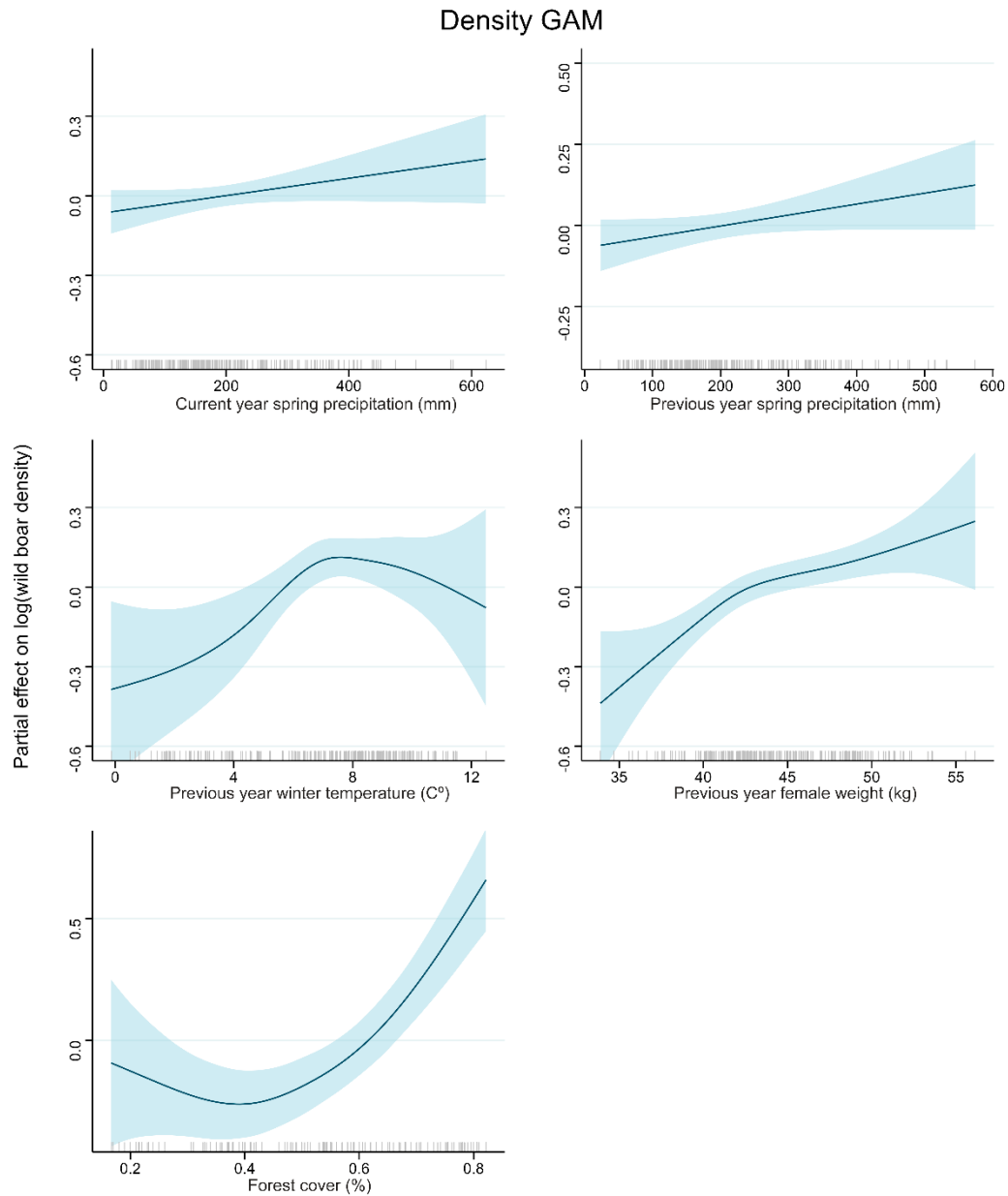


Figure 4.4. Effects of selected factors on wild boar density (expressed as the partial effect on log₁₀ density) in Catalonia derived from the results of generalized additive mixed models (GAMMs). The distribution of explanatory variable values is marked with grey vertical lines on the x-axis. The y-axis shows the predicted value of the response variable for a given predictor variable, while holding all other predictor variables at their average. Blue shadow represents the 95% confidence intervals.

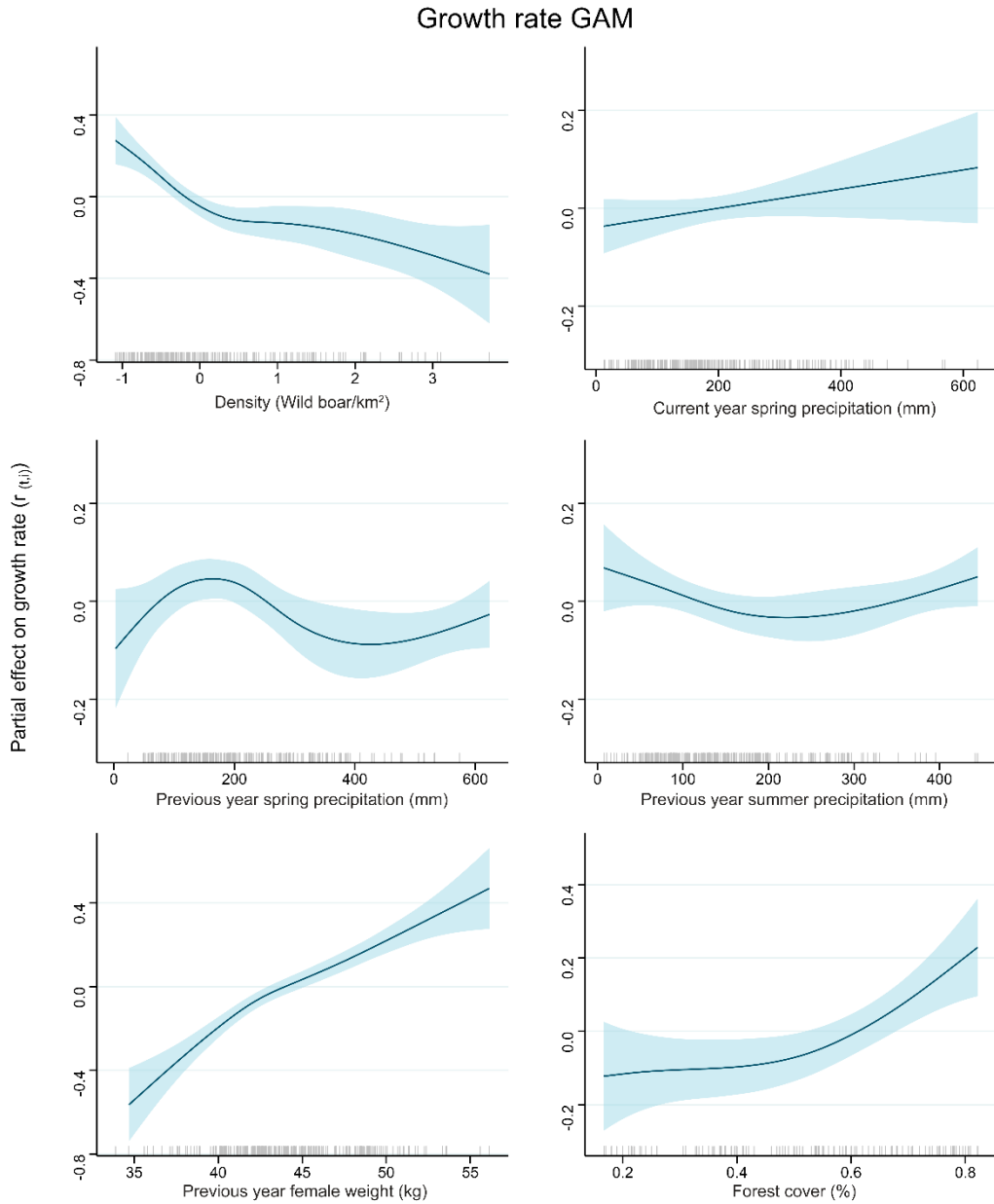


Figure 4.5.. Effects of selected factors on wild boar population growth rate ($r_{t,i}$, expressed as the partial effect on growth rate), in Catalonia derived from the results of generalized additive mixed models (GAMM). The distribution of explanatory variable values is marked with grey vertical lines on the x-axis. The y-axis shows the predicted value of the response variable for a given predictor variable, while holding all other predictor variables at their average. Blue shadow represents the 95% confidence intervals.

4 Discussion

By evaluating the main drivers of wild boar density and population dynamics, this research offers an in-depth understanding of the associations between meteorological, habitat and population factors on wild boar populations density and growth in Mediterranean ecosystems.

The results of the analyses indicate that spring precipitation (both from current and previous year), forest cover and female body weight are strongly associated with both wild boar densities and population growth. Summer precipitation and density of the previous year also appear to play a role in population growth. Moreover, density-dependence was detected and it may also play a relevant role in population dynamics.

In particular, spring precipitation and previous year spring precipitation were detected to be positively associated with both response variables (density and population growth) suggesting that drought conditions during the spring months may be a key limiting factor for wild boar, as hypothesized. This relationship could be attributed to increase of food and water available, leading to higher reproductive output, in terms of proportion of females reproducing and litter size, and higher piglet survival. The positive influence of previous year spring precipitation on wild boar density may be attributed to the heightened availability of food resources. Increased spring precipitation leads to a greater of mast and plant biomass production (Cutini et al., 2013; Espelta et al., 2008), which contributes to higher female body weight, and an increase of the reproductive output. These findings align with prior research conducted in southern Europe, which established that the number of rainy days during spring is a limiting factor for wild boar populations (Uzal Fernandez & Nores, 2004). This is also supported by the fact that our results show the association between mean female body weight from the previous year with both density and population growth, as hypothesized. The positive relationship between female body weight and reproductive output (and thus, population growth potential) has been described in previous papers on wild boar (Aumaitre et al., 1982; Cellina, 2008; Frauendorf et al., 2016; Lombardini et al., 2014; Mauget, 1972; Rosell et al., 2012). Moreover, changes in food availability can also affect on the timing of mating, the age of puberty and the sex ratio of the offspring, which in turn affect

population dynamics (Cachelou et al., 2022; Drimaj et al., 2020; Malmsten et al., 2017; Malmsten & Dalin, 2016).

Conversely, the positive association of spring precipitation in the current year on population density could be explained through effects on survival, especially of younger individuals. Given that the majority of wild boar birth occur during March and April, (Fonseca et al., 2011; Rosell et al., 2012), moisture content of soil during spring plays a crucial role in facilitating piglet foraging and access subterranean food resources once they are weaned. Low rainfall can prevent access to these food resources and subsequently negatively affect piglet survival (England, 1986; Fernández-Llario & Carranza, 2000; Fraser & Phillips, 1989; Phillips et al., 1990). Additionally, water shortages could reduce female milk production, thereby reducing piglet survival during the initial weeks of life, as demonstrated in other ungulates (Cain III et al., 2006).

These results imply that spring precipitation plays a key role in wild boar population dynamics in Mediterranean areas. Given the predicted decrease in precipitation levels in these regions over the next decades (Zittis et al., 2019) due to global warming, this may limit wild boar populations in drier areas and cause a shift of populations to higher and wetter areas within the region. However, wild boar residing in the proximity of agricultural and urban areas may increasingly rely on anthropogenic food (such crop and urban waste), thus making their energy requirements independent of weather conditions. This, in turn, will lead to an escalation of human-wild boar conflicts.

In terms of habitat composition, our study identified forest cover as an important variable associated wild boar density, while crop cover showed no clear relationship. However, the proportion of crop and forest cover are partially mutually exclusive, which might explain why only one of these variables (forest cover) was associated with wild boar density. These results may suggest that forest habitats remain the most favorable for wild boar populations in Catalonia, with a relationship showing a sharp increase in wild boar density when forest cover exceeded 60%. Similar results were found in previous studies but in more continental climate; for example, Borowik et al. 2013 reports higher wild boar densities in woodland cover above 40-50%. On the other hand, another study in Poland reported that the number of harvested wild boars was correlated positively to the increasing of maize crops surface (Kopij & Panek, 2016). In

Catalonia, the highest densities of wild boar have historically been recorded in large, continuous forests, although it is likely that crops provide an alternative food source, particularly during drought periods or in years of low production of forest fruits.

The population growth model shows a negative relationship between wild boar density of previous year and population growth. This finding implies Catalanian boar have negative density-dependence, where higher densities can limit but not suppress population growth, likely due to intraspecific competition for resources. Negative density-dependent processes have been widely described in other ungulates, such as moose, chamois or deer (Brown, 2011; Capurro et al., 1997; Coulson et al., 2000), and for wild boar (Imperio et al., 2012; Kapota & Saltz, 2018; Vetter et al., 2015). Other studies investigating wild boar dynamics found only weak density dependence, suggesting that this factor is unlikely to limit wild boar population growth (Bieber & Ruf, 2005; Choquenot, 1998; Frauendorf et al., 2016; Vetter et al., 2020), especially at the current stage of wild boar populations in Catalonia, which are assumed to be far from carrying capacity. Uzal Fernandez & Nores (2004) highlighted the apparent contradiction of assuming intraspecific competition for resources in populations that are still increasing in numbers, particularly in species like wild boar, with highly varied diet. Nevertheless, the variability in environmental factors could produce rapid changes in resource availability from one year to another in certain areas, resulting in increased or decreased intraspecific in-situ competition and subsequent density-dependence (Choquenot, 1998; Massei et al., 1997). In temperate climates with high population densities, intraspecific competition increases winter mortality and reduces fecundity rate in ungulates like chamois (*Rupicapra rupicapra*) and roe deer (*Capreolus capreolus*) (Capurro et al., 1997; Coulson et al., 2000). Density dependence can also affect sex ratio when food resources are limited (Frauendorf et al., 2016) and influence the age of sexual maturity and pregnancy rate among ungulates such as red deer (*Cervus elaphus*) (Clutton-Brock et al., 1986; Kruuk et al., 1999), or affect daily activity patterns for red deer, roe deer and wild boar (Ramirez et al., 2021).

One of the limitations of this study was the lack of data on the availability of natural food resources, as there are no consistent records on forest fruit production or other food sources. The second limitation was the impossibility to use the

number of wild boar hunted as an indicator for mortality, as the number of individuals hunted is one of the parameters employed for calculating density and thus could not be included as an explanatory variable. Finally, the complex nature of our models, combined with the relatively limited sample size and number of factors potentially affecting population density and growth poses a risk of overfitting, implying that the models may excessively capture noise of training data, and its performance in new scenarios should be interpreted carefully. So that, our work should be seen as an exploration of the relevant variables for our study area and conditions which may also be relevant in other situations and are worth to be further studied.

In conclusion, our results provide key insights into the effects of climate, landscape and population factors on wild boar population dynamics in Catalonia, with significant implications for wild boar population management. While meteorological factors cannot be directly controlled, our findings will contribute to elaborate more accurate population predictions based on the interaction of different climate variables for local populations in global change scenarios. Accurate predictions are essential for anticipating and planning management strategies, such as adjusting hunting efforts, implementing alternative methods to culling in conflict areas, or identifying key areas for habitat management and conservation.

Moreover, the limitation by spring precipitation shown by our results, which is likely to affect natural resources availability, is predicted to be more important during the next decades as precipitation is predicted to decrease in mediterranean areas. Due to the high adaptability of this species, the reliance of wild boar on human-related food (such crop, urban waste or domestic animals food) is likely to increase. Anthropogenic food provides wild boar with highly nutritious resources that improve female fitness (Castillo-Contreras et al., 2021) and subsequently the reproductive output of the populations. Additionally, urban food resources and crops provide a more stable food supply, independent of weather conditions, that may be particularly relevant for populations residing near agricultural and urban areas, thereby increasing the likelihood of wild boar-human conflicts.

Therefore, effective management measures to reduce anthropogenic food availability are crucial for mitigating conflicts and controlling population growth.

These measures can include preventing access to anthropogenic through crop field fencing or other exclusion measures, securing garbage bins and prevent access of wild boar to domestic animal food, contributing to limit reproductive output, which is directly related to female body weight. Habitat management and reducing refuge areas for wild boar in urban areas might also contribute to mitigate potential conflicts.

Finally, density-dependence processes also appeared as relevant factors in affecting population growth rate, but further research is needed to investigate the underlying mechanisms, including the potential impact of factors such as predation, diseases, and climate change.

5 Acknowledgements

This research is based on the data from the Catalan Wild Boar Monitoring Program, funded by the Catalan Government, Barcelona Regional Council (Diputació de Barcelona), Zona Volcànica de la Garrotxa Natural Park and Gavarres consortium. Special thanks to the hunting teams, technicians, rangers and site coordinators that collaborate with the data collection and management. We thank Simon Croft for his contributions on conceptualization and statistical analysis advise and our colleagues from Minuartia who provided valuable contributions that greatly assisted the research.

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Chapter 2.

Evidence of density-dependence in wild boar reproduction

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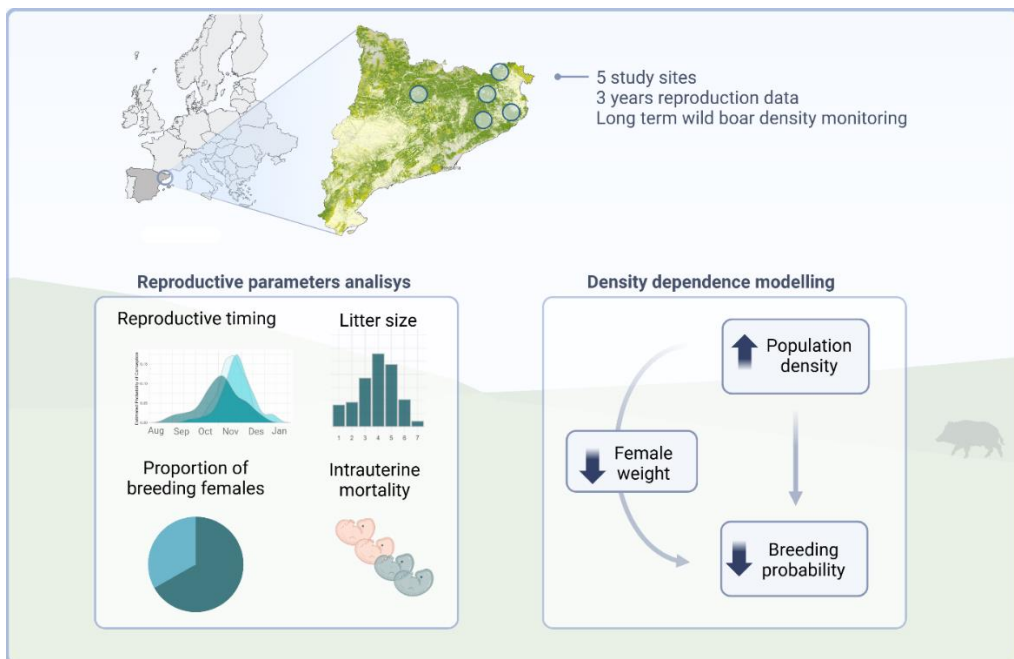
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Submitted in: Colomer, J., Rosell, C., Rodríguez-Teijeiro, J.D. & Massei, G. Submitted.
Evidence of density-dependence in wild boar reproduction. Biological Conservation.

Highlights

- Reproductive parameters were assessed across three years and multiple sites
- Proportion of breeding females the most variable reproductive parameter
- Female body weight influences reproductive success, affecting several parameters
- High population density reduces breeding probability, causes are poorly understood
- Other reproductive parameters –fertility, litter size- remain unaffected by density
- Body weight partly mediates density effects, but other factors play a role
- Long-term datasets are crucial for detecting density effects on reproduction

Graphical Abstract



Keywords

Density-dependence; Breeding probability; Reproduction; Population dynamics; *Sus scrofa*; Long-term monitoring

Abstract

Understanding the reproductive dynamics of wild boar populations is essential for developing effective management and conservation strategies. This study examines key reproductive parameters—ovulation rate, litter size, intrauterine mortality, and breeding probability—and their relationship with density across five Mediterranean sites over three years, using data from 575 females. Generalized linear mixed models (GLMMs) assessed the effects of population density on reproductive parameters while structural equation models (SEMs) explored density-dependent mechanisms. A long-term dataset spanning 23 years was used to further explore the relationship between density and female body weight. Results show that higher densities are associated with lower breeding probability, while ovulation rate, litter size, and intrauterine mortality were unaffected, suggesting that the primary reproductive adjustment to varying population densities lies in whether or not a female becomes pregnant, rather than the number of offspring produced. Female body weight influenced all reproductive parameters except intrauterine mortality. Short-term dataset analysis do not reveal any density effect on female body weight, while long-term dataset showed that higher population density is associated to reduced female body weight, highlighting the importance of long-term datasets in identifying processes that short-term studies might overlook. SEM also revealed a direct effect of density on breeding probability, independent of female body weight which may reflect density-dependent changes in other aspects (such physiology or behaviour) which ultimately influence reproduction. Our findings highlight the complex relationship between population density and reproductive success in wild boar and offer valuable information for understanding population dynamics and informing adaptative management.

1 Introduction

Wild boar (*Sus scrofa*) has emerged as a species with significant environmental and economic impacts across Europe, with populations expanding rapidly in recent decades (Apollonio et al., 2010; Massei et al., 2015). This expansion has led to increased human-wild boar conflicts which include crop damage, vehicle collisions, and disease transmission risks among others (Barrios-Garcia & Ballarí, 2012; Ruiz-Fons, 2017; Schley & Roper, 2003). The rapid range expansion and population growth of wild boar are driven by a combination of extrinsic and intrinsic factors. Extrinsic factors include changes in land use, agricultural practices, climate conditions, and declining hunter numbers (Apollonio et al., 2010; Vetter et al., 2015; Massei et al., 2015). Intrinsic factors, include the species' remarkable plasticity to adapt to diverse habitats and changing environment and resource availability, but also the exceptionally high reproductive potential, being the ungulate with the highest reproductive outputs (Focardi et al., 2008). Understanding the factors affecting reproduction in this species is thus crucial for predicting population trends and for effective population management, particularly in areas characterised by rapidly changing environmental conditions (Bieber & Ruf, 2005; Gamelon et al., 2017).

Wild boar reproduction is characterized by high fecundity and early sexual maturity and displays remarkable plasticity that allows the species to quickly adjust reproductive output to local conditions. This flexibility is particularly evident in Mediterranean ecosystems, where resource availability may undergo significant fluctuations (Fernández-Llario & Carranza, 2000; Massei et al., 1997; Rosell, 1998, 2012). Such adaptability drives its exceptional potential for rapid population growth, allowing it to take advantage of available resources. In years of high resource availability, this flexibility allows substantial population growth, which can lead to overpopulation and complicate efforts for population control. The reproductive plasticity of wild boars has been extensively studied, with findings highlighting how environmental factors such as resource availability, climate, and habitat conditions modulate key reproductive parameters (Cachelou et al., 2022; Drimaj et al., 2020; Frauendorf et al., 2016; Gamelon et al., 2017; Servanty et al., 2007, 2009). In Mediterranean regions, average litter size for wild boar typically is around 4 piglets per female, with a range between 2.3 and 5.6 (Brogi et al., 2022; Focardi et al., 2008; Massei et al., 1997; Rosell et al.,

2012). In northeastern Iberian Peninsula, where our study areas are located, litter size has been reported to range between 3.78 ± 0.27 (Rosell, 1998). In contrast, wild boar occurring at higher latitudes such as in Central and Northern Europe often exhibit larger litter sizes, with averages ranging from 4.6 to 6.9 piglets (Gethöffer et al., 2007; Náhlik & Sándor, 2003). Bywater et al. (2010) reported a positive relationship between litter size and latitude, with an increase of approximately 0.15 piglets per degree of latitude, which represents one of the first documented cases of this phenomenon in a large mammal species. Proportion of breeding females, which is another main reproduction parameter, also shows considerable variation. In central and northern Europe, studies have reported proportion of breeding females ranging from 60% to 95% in adult females, depending on environmental conditions and population age and class structure (Gethöffer et al., 2007; Mauget, 1972; Pépin et al., 1986; Servanty et al., 2009). In Mediterranean areas, proportion of breeding females have been reported to be particularly sensitive to resource availability, with studies reporting ranges from 17% to 85% depending on mast production (Fernández-llario & Carranza, 2000; Massei et al., 1997; Rosell et al., 2012).

Regarding factors influencing reproductive success, multiple studies have found positive relationships between female body weight and reproductive parameters such as litter size, ovulation or breeding probability (Aumaitre et al., 1982; Drimaj et al., 2020; Gaillard et al., 1993; Gethöffer et al., 2007; Mauget, 1972). Body condition also influences the beginning of puberty, as wild boar females typically reach sexual maturity at a threshold body mass of approximately 30 kg (Aumaitre et al., 1982; Rosell, 1998). Pregnant females at lower body weight (20-25kg) have also been reported in study areas where supplementary feeding was available (Servanty et al., 2009). This finding suggests that favourable environmental conditions leading to rapid growth can result in earlier reproduction, potentially accelerating population growth. Conversely, poor resource availability may delay sexual maturity, serving as a natural regulatory mechanism (Gamelon et al., 2013). The timing of reproduction in wild boar is also subject to environmental influences, demonstrating the species' ability to adjust its reproductive phenology in response to resource availability (Mauget, 1982). Mating activity usually peaks in November, but it can vary depending on mast availability (Cachelou et al., 2022; Canu et al., 2015; Gamelon et al., 2021; Mauget, 1982).

While the impacts of environmental factors on wild boar reproduction have been well-documented, the role of density dependence has received limited attention. Two potential mechanisms through which density dependence can act have been described for wild boar. Firstly, high population density could lead to increased competition for resources, affecting body condition and, consequently, reproductive output (Focardi et al., 2008; Servanty et al., 2009). In other ungulate species, such as the roe deer (*Capreolus capreolus*), population density has been described as a body size regulator, with higher densities being associated with smaller individuals, in response to stronger competition for food resources (Festa-Bianchet et al., 1998; Morellet et al., 2007). Alternatively, density-dependent effects might manifest through changes in social structure, home-range, behaviour, stress levels, or disease transmission rates, all of which could impact reproduction (Augustsson et al., 2024; Barasona et al., 2020; Focardi et al., 2008; Risco et al., 2014; Ruiz-Fons, 2017). However, the mechanisms underlying these effects remain unclear, and their implications for wild boar reproduction and population dynamics are still not fully understood.

Regarding the impact of density dependence on wild boar reproduction and population dynamics, some studies have found no significant density-dependent effects on population growth, fertility, or litter size (Choquenot, 1998; Ditchkoff et al., 2012; Frauendorf et al., 2016; Uzal Fernandez & Nores, 2004). Conversely, others found that density influences different parameters such as female body weight, population growth, conception date or disease-related mortality (Barasona et al., 2020; Bruinderink & Hazebroek, 1995; Imperio et al., 2012; McCullough, 1999; Risco et al., 2014; Ruiz-Fons, 2017; Vetter et al., 2015). A previous study in our study area, found that higher wild boar densities were associated with lower population growth in the following year but did not investigate population density effects on reproduction parameters (Colomer et al., 2024).

Understanding the mechanisms of density dependence on wild boar reproductive output is essential for predicting population dynamics and implementing adaptive management strategies in the face of changing environmental conditions and expanding wild boar populations. This study aims to clarify how density-dependent influence key reproductive parameters of a

Mediterranean wild boar population. Specifically, the objectives of this research are:

- To summarise data on reproductive parameters and mating periods across different sites and years in a Mediterranean region.
- To explore the density-dependent processes affecting the reproduction.
- To investigate the underlying mechanisms of these density-dependent effects, with the hypothesis that female body weight mediates these relationships.

2 Methods

2.1 Study area

The study sites are located in the northeastern part of the Iberian Peninsula, in Catalonia, Spain. This region is characterized by a Mediterranean climate, which varies significantly across the sites due to differences in elevation and proximity to the coast. The study area includes a range of elevations, from sea level to over 1,700 meters above sea level (m.a.s.l.), encompassing a diverse array of climatic conditions. The land cover includes a mix of forest, shrubland, and agricultural landscapes (Figure 4.6).

Five key sites were selected for this study: Alt Empordà, Gavarres, Montseny, Solsonès-Berguedà, and Garrotxa. These locations were chosen to represent a wide variety of microclimates and ecosystems within the Mediterranean zone, including coastal areas, interior mountain ranges, and volcanic landscapes. All study sites are mainly covered by dense forest (mean dense forest cover 53%), being the sclerophyllous evergreen species, such as *Quercus ilex*, *Quercus suber* and *Quercus humilis* the more dominant species. In the areas with higher precipitation, such as Montseny and Garrotxa, also chestnut (*Castanea sativa*) and beech (*Quecus sylvatica*) formations are frequent. In the lower areas, shrub formations based on species such as *Erica arborea*, *Spatium junceum*, and *Calicotome alba*, *Ulex parviflorus* and *Cistus species* are present in landscape mosaic together with forests and croplands.

The crop cover present mainly in lower areas, represents about the 3,8% of the study sites, with Gavarres being the site with a higher percentage (6%), and Alt Empordà the lower (1,4%).

The climatic data for each site were derived from the most representative meteorological station within the area, with rainfall and temperature data averaged over the past 10 years. Table 4.2 summarizes the key environmental characteristics and the number of collected samples at each site.

Table 4.2. Characteristics and number of collected samples of the 5 sites included in the analysis. Yearly rainfall and monthly temperatures correspond to the mean of the last 10 years (data from the Servei Meteorològic de Catalunya) and altitude range (ICGC, 2023)

Sites	Yearly rainfall (ml)	Mean temp. colder month (°C)	Mean temp. warmer month (°C)	Altitude range (m.a.s.l.)
Alt Empordà	732.4	7.5	23.8	53 - 1.451
Gavarres	516.5	7.3	24.1	0 - 532
Montseny	965.2	4.2	21.0	61 - 1.706
Solsonès-Berguedà	597.1	6.8	23.9	445 - 1.429
Garrotxa	1.029.1	5.5	22.4	136 - 1.513

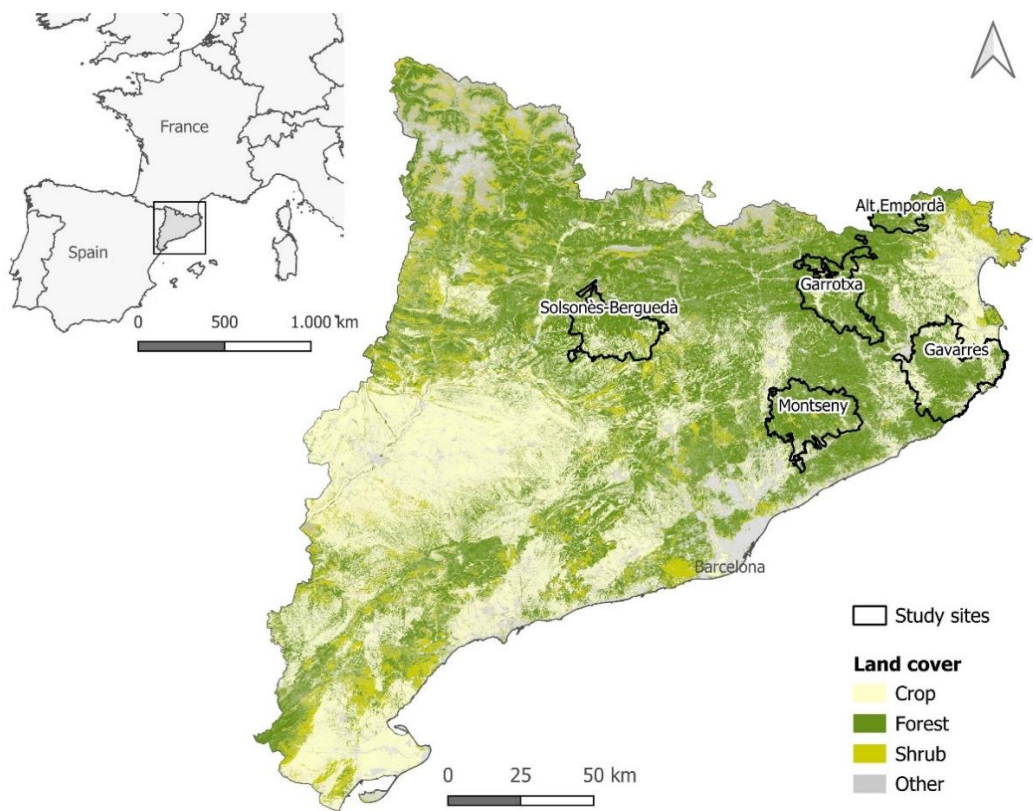


Figure 4.6. Study area (Catalonia, NE Spain), showing the 5 study sites where wild boar reproductive tracts were collected.

2.2 Data collection

A total of 575 female wild boar were collected in the 5 different study sites during three hunting seasons 2021/22 (year 2021), 2022/23 (year 2022) and 2023/24 (year 2023) (Table 4.3). For each site the density of wild boar was provided by the Catalan Wild Boar Monitoring Program, which is estimated via the method described in Colomer et al. (2024), based on driven hunts data considering the number of wild boars hunted, the hunting effectiveness (proportion of wild boar observed that are hunted) and the site surface.

Table 4.3. Number of samples and wild boar density (wild boar/km²) in each study site. NA indicates not available data.

Site	2021		2022		2023		N Samples Total
	N samples	Density	N samples	Density	N samples	Density	
Montseny	46	14.9	46	9.9	47	8.7	139
Garrotxa	45	14.4	39	12.4	50	10.8	134
Gavarres	31	12.9	31	7.6	44	NA	106
Alt Empordà	38	17.5	24	22.8	44	16.2	106
Sols.- Berguedà	40	4.3	24	5.6	26	4.6	90
Total	200		164		211		575

2.3 Analysis of reproductive parameters

The reproductive tracts (uteri and ovaries) were collected from November to January during 2021, 2022 and 2023. For each individual, live body weight (kg), date, and hunting ground were recorded. Samples were preserved in formaldehyde at 4°C. In the laboratory, the uteri were examined, fetuses of pregnant females were counted and sexed when the developmental stage allowed it, and the snout-to-tail base length (L) was measured in millimetres to estimate foetal age (A) and time at conception according to the method described by Vericad, (1981):

$$A=22.5378+0.2893L$$

Litter size was defined as the mean number of fetuses found per uterus. Ovaries were weighed, and ovulation rate was calculated as the mean number of corpora lutea found in both ovaries. Intrauterine mortality (IUM) was defined as the difference between the ovulation rate and litter size (Abaigar, 1992; Mauget, 1972):

$$IUM = \frac{\text{Ovulation rate} - \text{Litter size}}{\text{Ovulation rate}} * 100$$

Using the estimated foetal age and the culling date of the female, conception and birth dates for the litter were estimated (Mauget, 1972). The density distribution of conception dates was calculated using kernel density estimation (KDE) applied to the actual conception dates across three years (2021–2023). The KDE method was employed to smooth the raw data and generate an estimate of the probability of conception across different months. This analysis provided a visual representation of the temporal distribution of conceptions for each year.

The proportion of breeding females was calculated using data from December and January only. Samples collected in November were excluded, as the peak rut occurs in this month in our study area (Rosell, 1998), and some females may not yet be pregnant, potentially underestimating the real proportion of pregnant females. Therefore, the calculation is based on 493 of the 575 samples collected.

For ovulation rate, litter size, and intrauterine mortality, Kruskal-Wallis tests were conducted to assess differences across years and sites. This non-parametric test was chosen due to the non-normal distribution of data (Zar, 2010). For conception date distributions, the Kruskal-Wallis test was also used to analyse differences among years, and Dunn's post-hoc test with Bonferroni correction was applied to determine specific pairwise differences (Dunn, 1964). Statistical significance was set at $p < 0.05$, and all statistical analyses were conducted in R (R Core Team, 2023).

2.4 Modelling effects of population density and weight in reproductive parameters

The effects of population density on various reproductive parameters of wild boar were explored, including the number of corpora lutea, litter size, intrauterine mortality, and breeding probability. Linear mixed models (GLMMs) were fitted for each parameter.

For modelling the breeding probability, it was coded as 1 for breeding females and 0 for non-breeding females and modelled using a binomial distribution with a logit link function. We used the full dataset ($n = 575$) incorporating body weight (kg), current-year population density, and previous-year population density as fixed predictors. Random intercepts were included to account for variability

across sites and years. The random effects structure was assessed by examining the conditional variances, revealing that the random effect for year had minimal variance, suggesting negligible temporal variability. Consequently, the model with only the random intercept for site was selected as the final model, offering the best fit according to AIC and BIC, while capturing the key sources of variability.

For the corpora lutea, litter size and intrauterine mortality models, the same explanatory variables were used (female weight, current-year population density, and previous-year population density and site as a random factor). For the number of corpora lutea (luteal bodies), only samples of pregnant females were used ($n=264$), and a Poisson distribution was applied, as it is suitable for modelling count data representing discrete, non-negative events occurring independently. For the number of fetuses, only samples from pregnant females with no missing fetuses were included ($n=288$), excluding cases with incomplete uterus samples. A zero-inflated Poisson model was applied to account for the excess zeros. A likelihood ratio test (LRT) comparing the zero-inflated and non-zero-inflated models revealed a significant improvement in fit (Chi-squared = 195.15, $df = 1$, $p < 2.2e-16$), justifying the use of the zero-inflated Poisson model (Zeileis et al., 2008). In the intrauterine mortality model, only pregnant females with complete ovaries, uterus, and detectable fetuses were included ($n=171$). A Beta distribution was used for the response variable, as it represents proportions bounded between 0 and 1. To ensure all values were strictly within this range, 0 values were adjusted by replacing them with $1e-5$ (Ferrari & Cribari-Neto, 2004).

Before fitting the models, collinearity among predictors was evaluated. Pearson correlation coefficients were calculated, and predictors with absolute values greater than 0.7 were considered to exhibit strong collinearity, potentially problematic for model interpretation. The variance inflation factor (VIF) was also calculated, with values greater than 3 indicating potential multicollinearity. No predictors exceeded these thresholds, suggesting no significant issues with collinearity (Zuur et al., 2010).

2.5 Path analysis for breeding probability

To assess the mechanisms of density dependence and evaluate whether population density directly influenced pregnancy probability and whether this

effect was mediated by female body weight a series of structural equation models (SEM) were conducted using the piecewise SEM approach (Lefcheck, 2016). Using confirmatory path analyses (Shipley, 2009), four structural equation models (SEMs) were build, which tested different hypotheses about how body weight mediates the effects of population density on breeding probability. In all models, 'site' was included as a random factor, recognizing the spatial heterogeneity of the population and accounting for potential within-location correlations that might otherwise lead to inflated type I error. However, 'year' was excluded as a random factor from the models due to issues with singularity. This occurred because the variance of the random effect for year was effectively zero, indicating that there was no meaningful variation across seasons in the dataset. So that, 'year' was excluded to avoid overfitting and ensuring that random effects remained interpretable.

We assessed whether the variation breeding probability: (1) depends directly on female body weight and indirectly on current year wild boar density, with body weight mediating the density effect (2) depends directly on female body weight and is directly influenced by current year wild boar density, without body weight mediation (3) depends directly on female body weight and is directly influenced by both current and previous year wild boar density, without body weight mediation and (4) depends directly on female body weight and indirectly influenced by both current and previous year density, through body weight.

The four global models included all potential relationships between these variables, allowing for direct effects of body weight on pregnancy probability and density effects on body weight and pregnancy probability. Fisher's C statistic was calculated to assess model fit, with p-values indicating whether the models adequately represented the data. All models showed p-values greater than 0.05, indicating a good fit. To select the best model, the goodness of fit for each model were compared using the Akaike Information Criterion (AIC), considering AIC values corrected for small sample size (AICc) when appropriate. The model with the lowest AICc was selected as the best-fitting model and is the one presented in the results (Table 4.4). The other models are ranked by their $\Delta AICc$ values, with values closer to zero indicating a better fit to the data.

Table 4.4. Model fit for the 4 best global models, including the number of parameters, the AICc of the four best models, and the difference between each tested model and the best one. The variables included are breeding probability (P), female body weight (W), current year population density (D) and previous year population density (D_{t-1}), and site (S) as a random factor.

Model notation	N parameters	AICc	ΔAICc
$P \sim W + D_t + D_{t-1} + (1 S); W \sim D_t + (1 S); D_t \sim D_{t-1} + (1 S)$	11	7413.69	
$P \sim W + D_t + D_{t-1} + (1 S); W \sim D_t + D_{t-1} + (1 S); D_t \sim D_{t-1} + (1 S)$	12	7450.51	-36.82
$P \sim W + D_t + (1 S); M \sim D_t + (1 S); D_t \sim D_{t-1} + (1 S)$	10	7452.66	-38.96
$P \sim W + (1 S); M \sim D_t + (1 S); D_t \sim D_{t-1} + (1 S)$	9	7453.47	-39.78

To ensure the robustness of our conclusions, model's goodness-of-fit were evaluated by inspecting Chi-squared statistics, degrees of freedom, and p-values. For each model, the standardized regression coefficients (scaled by mean and variance) and their associated standard errors (SE) were examined. This allowed us to quantify the relative strength of relationships among the variables. The model's explanatory power was evaluated by calculating the R-squared values for each response variable, considering both marginal and conditional estimates. The assumptions of normality and residuals were tested using the Shapiro test and visual inspections such as Q-Q plots.

2.6 Long-term analysis of density effects on female body weight

To further assess the effect of density in female body weight, we performed a secondary analysis using a larger, long-term dataset from the Wild Boar Monitoring Program (Colomer, 2023). This dataset, spanning 23 years and 20 different sites in the same region, allowed for a more robust examination of the relationship between population density and body weight. Two separate generalized linear mixed-effects models (GLMMs) were fitted with a Gaussian distribution to assess the effect of current (D_t) and previous year (D_{t-1}) population densities on female body weight (W). Given the high correlation between current and previous year density ($r = 0.91$), we chose to model them separately to avoid multicollinearity. Both models included site (S) and year (Y) as random effects to account for spatial and temporal variation in the data: Model 1: $W \sim D_t + (1 | S) + (1 | Y)$ and Model 2: $W \sim D_{t-1} + (1 | S) + (1 | Y)$. The fixed effects were assessed for significance using Wald chi-square tests on the deviance of the models, with p-values obtained employing Type III sums of squares.

All analyses were performed using R, version 4.2.1 (R Core Team, 2022), with packages *piecewiseSEM* (Lefcheck, 2016) and *lavaan* (Rosseel, 2012) for

structural equation modelling, *MuMIn* (Bartoń, 2024) for model comparison, and *car* (Fox et al., 2024) for model diagnostics and *lme4* (Bates et al. 2015) for model building.

3 Results

3.1 Reproductive parameters

A total of 575 female reproductive tracts were analysed and 329 were found pregnant, meaning that 60% of the total females were breeding. Proportion of breeding females show a wide range of variability, ranging from 29% to 81% in the 5 study sites and 3 periods analysed. Significant differences in the proportion of breeding females were found across years ($\chi^2 = 23.619$, $p < 0.001$), but not across sites ($\chi^2 = 4.00$, $p = 0.41$) (Table 4.5).

Table 4.5. Reproductive parameters and female body weight for each year and study site. Standard errors are presented in parentheses.

Year	Alt Empordà	Gavarres	Montseny	Solsonès-Berguedà	Garrotxa	TOTAL
2021						
Prop. breeding females ¹	74%	58%	41%	73%	80%	65%
$\bar{X}$ C. lutea (SE)	4,7 (0,3)	4,1 (0,4)	4,2 (0,2)	4,4 (0,2)	4,3 (0,2)	4,4 (0,1)
$\bar{X}$ Litter size (SE)	4,1 (0,4)	3,8 (0,4)	4,1 (0,2)	4,0 (0,2)	4,2 (0,2)	4,1 (0,1)
$\bar{X}$ Intr. Mortality (SE)	17% (0,1)	16% (0,1)	3% (<0,0)	15% (<0,0)	4% (<0,0)	10% (<0,0)
$\bar{X}$ F Body weight (SE)	42,0 (1,7)	41,5 (1,6)	55,1(1,9)	48,4 (1,5)	43,9 (1,6)	46,6 (0,8)
2022						
Prop. breeding females ¹	29%	39%	41%	71%	33%	42%
$\bar{X}$ C. lutea (SE)	4,3 (0,4)	4,3 (0,4)	4,1 (0,4)	4,4 (0,4)	4,4 (0,4)	4,3 (0,2)
$\bar{X}$ Litter size (SE)	3,9 (0,4)	3,4 (0,5)	3,6 (0,3)	3,5 (0,4)	4,0 (0,9)	3,6 (0,2)
$\bar{X}$ Intr. Mortality (SE)	12% (0,1)	31% (0,1)	11% (0,1)	22% (0,1)	2% (0,1)	19% (<0,0)
$\bar{X}$ F Body weight (SE)	46,3 (3,2)	44,1 (2,4)	45,4 (2,6)	48,3 (1,7)	41,1 (1,8)	44,7 (1,1)
2023						
Prop. breeding females ¹	63%	88%	80%	53%	84%	75%
$\bar{X}$ C. lutea (SE)	4,8 (0,4)	5,0 (0,3)	4,7 (0,2)	4,7 (0,4)	4,5 (0,2)	4,7 (0,1)
$\bar{X}$ Litter size (SE)	3,4 (0,4)	4,0 (0,4)	4,3 (0,2)	3,8 (0,6)	3,9 (0,5)	4,0 (0,2)
$\bar{X}$ Intr. Mortality (SE)	30% (0,1)	21% (0,1)	11% (<0,0)	19% (0,1)	26% (0,1)	20% (<0,0)
$\bar{X}$ F Body weight (SE)	43,9 (2,2)	45,8 (2,2)	45,5 (2,2)	38,7 (2,8)	44,8 (1,6)	44,2 (1,0)
Total						
Prop. breeding females ¹	58%	59%	54%	67%	64%	60%
$\bar{X}$ C. lutea (SE)	4,7 (0,2)	4,6 (0,2)	4,4 (0,1)	4,4 (0,2)	4,4 (0,1)	4,5 (0,1)
$\bar{X}$ Litter size (SE)	3,8 (0,2)	3,8 (0,3)	4,1 (0,1)	3,8 (0,2)	4,1 (0,2)	3,9 (0,1)
$\bar{X}$ Intr. Mortality (SE)	21% (<0,0)	21% (<0,0)	9% (<0,0)	18% (<0,0)	13% (<0,0)	16% (<0,0)
$\bar{X}$ F Body weight (SE)	43,8 (1,3)	44,1 (1,2)	48,6 (1,3)	45,5 (1,3)	43,4 (0,9)	45,2 (0,6)

¹Samples collected during November have not been included in the calculation of this parameter.

The seasonal distribution of conception dates (Figure 4.7), derived from foetal age data, reveals distinct patterns across the years. In 2021 and 2022, mating peaked in the third and fourth week of November, starting in September and continuing until final-January. However, in 2023 mating began approximately two weeks earlier, peaking in the first week of November, starting in August and extending until mid-January. Correspondingly, birth periods exhibited similar distributions, with the highest number of births occurring in March. Analysis of conception dates, using data from all years without differentiation by site, indicated significant differences across years ($\chi^2 = 28.37$, $df = 2$, $p < 0.001$); the distribution in 2023 significantly differed from that in 2021 ($Z = 3.56$, $p < 0.001$) and 2022 ($Z = 5.16$, $p < 0.001$), while no significant difference was observed between 2021 and 2022 ($Z = -2.04$, $p = 0.062$).

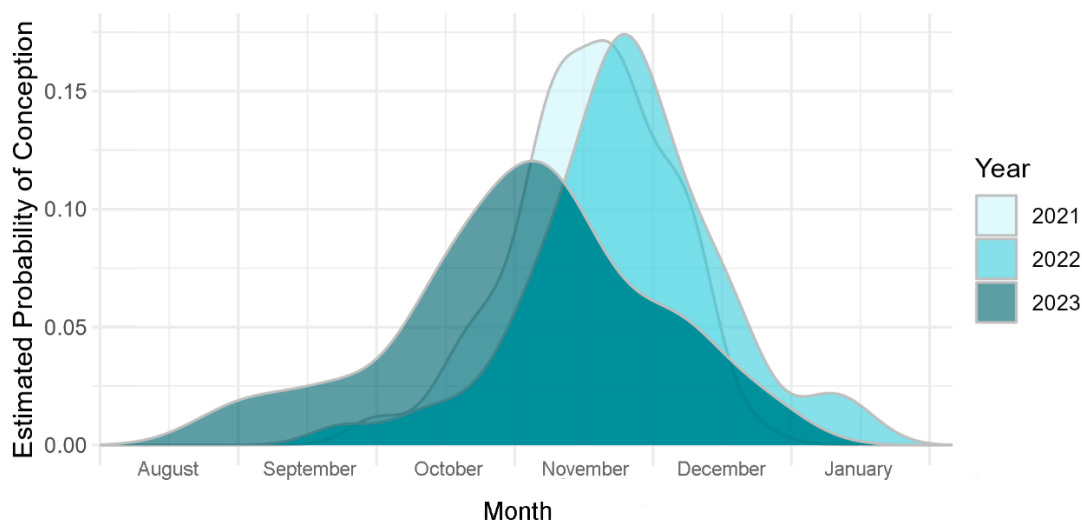


Figure 4.7. Density distribution of conception dates, showing the estimated probability of conception across different months of the study period. Distribution was calculated using kernel density estimation on conception dates extrapolated from foetal age.

Across the three monitored years, the global mean ovulation rate was 4.5 (SE = 0.1). In 2021, it was 4.4 corpora lutea per female (SE = 0.1), 4.3 (SE = 0.2) in 2022, and 4.7 (SE = 0.1) in 2023. No significant differences in ovulation rate across sites for all years combined were detected ($\chi^2 = 1.54$, $df = 4$, $p = 0.82$). Additionally, no significant differences were found between years at individual sites (all p -values > 0.05), nor when comparing all sites together across years ($\chi^2 = 2.64$, $df = 2$, $p = 0.27$).

The global mean litter size was 3.9 (SE = 0.1) foetuses per female, with 4.1 (SE = 0.1) foetuses in 2021, 3.6 (SE = 0.2) in 2022, and 4.0 (SE = 0.2) in 2023 (Figure 4.8).

No significant differences in litter size across locations in any of the three years were detected (Kruskal-Wallis test; all p-values > 0.05), nor across sites for all years combined (Kruskal-Wallis test; $\chi^2 = 1.96$, df = 4, p = 0.74). Differences among years within each study site were also not detected (Kruskal-Wallis test; all p-values > 0.05). These results indicate consistent litter sizes across both years and locations.

Regarding intrauterine mortality, the global mean was 0.16, meaning that, on average, 16% of foetuses were lost relative to the number of corpora lutea. No significant differences in intrauterine mortality were observed between sites in any year (Kruskal-Wallis test; all p-values > 0.05). When testing differences within individual sites across seasons, only one site, Garrotxa, showed a significant variation among years ($\chi^2 = 8.46$, df = 2, p = 0.015), while the remaining sites exhibited no significant differences (Kruskal-Wallis test; all p-values > 0.05).

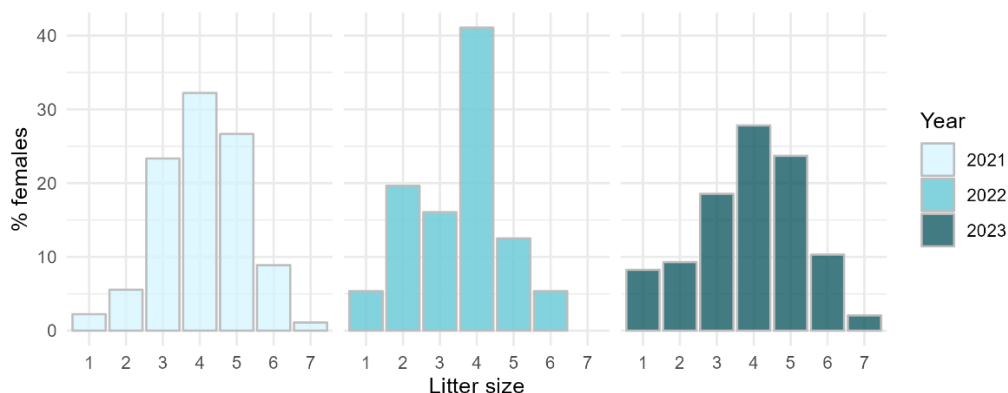


Figure 4.8. Frequency distribution of the number of foetuses per female across years in each study site. Each panel represents data for one year, showing variation in the number of foetuses observed per female.

3.2 Effects of population density in reproductive parameters

Results from the generalized linear mixed models (GLMMs) show a significant negative effect of population density in the breeding probability, indicating a density dependent effect (Table 4.6 and Figure 4.9). On the contrary, no significant effect of population density is found on the number of corpora lutea, litter size, or intrauterine mortality (Supplementary Materials, Tables A1, A2, and A3). Female body weight appeared as a significant factor in all models except for intrauterine mortality, showing a positive relationship with both the number of corpora lutea and litter size (Supplementary Materials, Tables A1, A2, and A3), and having a significant positive effect on breeding probability.

Table 4.6. Results of the GLMM, including female weight (W), current year population density (D_T) and previous year density (D_{T-1}) as explanatory variables, and study site as a random factor. The model included all observations ($n=575$). The variance explained by both fixed and random variance is $R^2_c = 0.69$. Significance codes: '***' $p < 0.001$.

Predictors	Estimate	SD	Z value	Pr(> z) value	Effect
W - Female body weight	0.07194	0.00914	7.871	3.52e-15 ***	Increased breeding probability with higher female body weight
D_T - Current year Population density	-0.19012	0.04216	-4.510	6.49e-06 ***	Decreased breeding probability with higher population density
D_{T-1} - Previous year density	-0.27313	0.04316	-6.328	2.49e-10 ***	Decreased breeding probability with higher population density during the previous year
Random effect	Variance	Std. Dev			
Site	3.019	1.737			
Response variable					
Breeding probability	-				
Binomial					

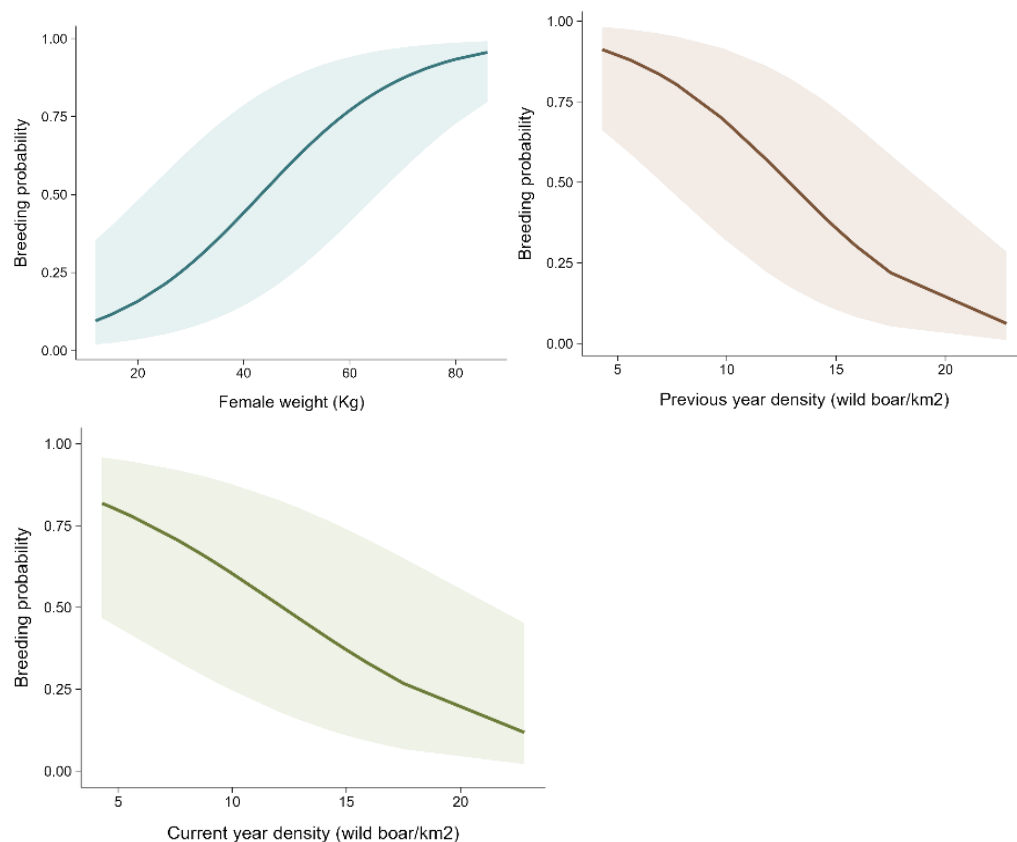


Figure 4.9. Effect of female weight (kg), previous and current year density (wild boar/km²) on female wild boar breeding probability as predicted by the selected best GLMM. Color-shaded areas represent 95% confidence intervals.

3.3 Path model of breeding probability

The best path model using structural equation modelling (AICc = 7413.69) revealed a significant negative direct effect of population density—both from the current and previous year—on breeding probability (Figure 4.10). The path model showed a good fit to data, as indicated by the Chi-squared test ($\chi^2 = 0.23$, $df = 1$, $p = 0.64$) and Fisher's C test (Fisher's C = 3.35, $df = 2$, $p = 0.19$) (Supplementary Materials, Tables A4). A significant positive effect of female body weight on breeding probability was also observed. Interestingly, the path model didn't show any significant direct effect of current density on female body weight, suggesting that other factors may be involved in the relationship between density and breeding probability.

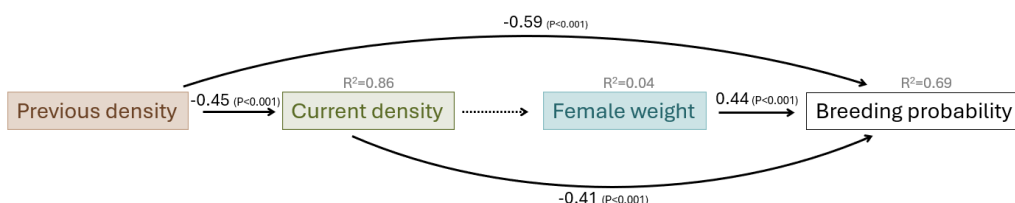


Figure 4.10. Selected path models for the breeding probability. Continuous lines represent significant relationships, dotted lines represent non-significant relationships. Standardized coefficients and p values are shown for each relationship. The explained variation (R^2) is shown for each response variable.

3.4 Long-term analysis of density effect on female body weight

Although no significant relationship between density and female body weight was detected in the primary path analysis based on the 3 years dataset, the models including a long-term dataset revealed that female weight is indeed significantly influenced by population density (Table 4.7, Figure 4.11).

In this long-term analysis, both models included female body weight (W) as the response variable, and site as a random factor. The first model revealed a significant negative effect of current population density on female body weight (Estimate = -0.19, SE = 0.066, $t = -2.89$, $p = 0.004$). The second model, which assessed the effect of previous year density, did not show a significant effect on female body weight, although shows a p -value approaching significance (Estimate = -0.12, SE = 0.066, $t = -1.818$, $p = 0.069$).

Random effects revealed substantial variation between sites (Variance = 7.10, Std. Dev. = 2.66 for the first model; Variance = 7.78, Std. Dev. = 2.79 for the second

model), with smaller variation between years (Variance = 0.50, Std. Dev. = 0.71 for the first model; Variance = 0.47, Std. Dev. = 0.69 for the second model). The residual variance was 6.86 (Std. Dev. = 2.62) for the first model and 6.68 (Std. Dev. = 2.58) for the second model. The REML criterion at convergence was 1381.3 for the first model and 1302.4 for the second model.

*Table 4.7. Results of the two GLM including female weight (W) as predictor, the first model (n=278) included current year density (D_t) as explanatory variable, and the second (n=263) the previous year density (D_{t-1}), and site as a random factor. Significance codes ‘***’ $p < 0.01$.*

MODEL 1					
Predictors	Estimate	SD	t value	Pr(>Chisq)	Effect
D _t -Current year population density	-0.191	0.066	-2.89	0.004 **	Decreased female weight with higher population density
Random effect	Variance	Std. Dev			
Site	7.096	2.664	Considerable site-specific variation in female weight Low year-level variation in female weight		
Year	0.507	0.711			
Response variable					
Female weight (kg)					
MODEL 2					
Predictors	Estimate	SD	t value	Pr(>Chisq)	Effect
D _{t-1} -Previous year population density	-0.121	0.066	-1.818	0.069 .	No significant effect
Random effect	Variance	Std. Dev			
Site	7.778	2.789	Considerable site-specific variation in female weight Low year-level variation in female weight		
Year	0.473	2.585			
Response variable					
Female weight (kg)					

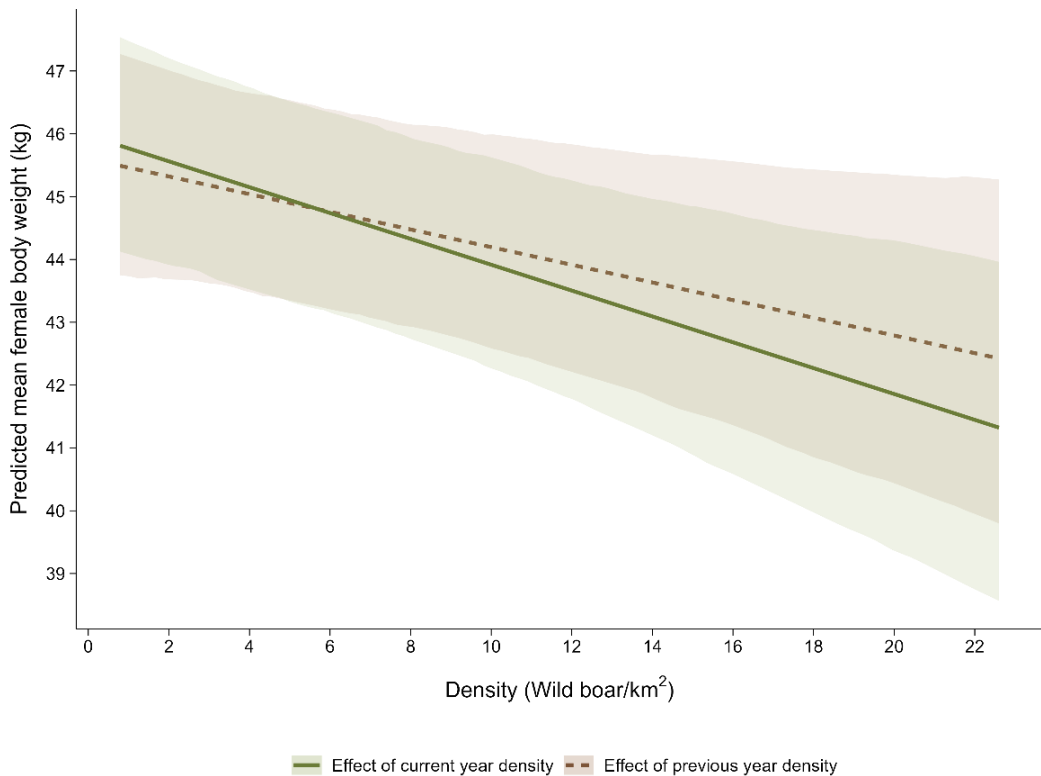


Figure 4.11. Effect of current year (significant) and previous year (marginally significant) densities on female body weight. Colour-shaded areas represent 95% confidence intervals.

4 Discussion

The study shows the density-dependent effects on wild boar reproduction. Through path analysis and long-term data, we demonstrate that density significantly affects reproductive dynamics, with higher densities linked to lower breeding probability. We found that this process is partially mediated through female body weight, as a negative effect of current year density on female weight was detected in long-term datasets, which was not observed in shorter datasets. Nevertheless, other mechanisms, such as physiological, social, and behavioural aspects linked to density variations, are also likely to play a key role. We also describe key reproductive parameters, including mating period, litter size, and breeding probability.

We also describe key reproductive parameters, including mating period, litter size, and breeding probability. Our findings indicate an earlier and wider mating period in 2023 compared to previous years. We hypothesize that the dry conditions of 2023, following another severe drought in 2022, reduced resource availability, which likely led to an advancement and extension of the mating

period. This hypothesis aligns with the results of Fernández-Llario and Mateos-Quesada (2005), which showed that dry summers in Spain may induce earlier conception. However, many other studies have found that low resource availability generally results in later reproduction (Aumaitre et al., 1984; Brogi et al., 2022; Cachelou et al., 2022; Canu et al., 2015) suggesting that drought and resource limitation in different regional ecological contexts can lead to have different effects on reproductive timing. Regarding the duration of the reproductive period, studies suggest that low-resource environments may extend mating periods and lead to less synchronous breeding, which mirrors our findings (Brogi, 2022). Additionally, social dynamics may also play a role, as noted by Canu (2015), who observed that sows sampled in the same area and year exhibited similar reproductive timing, suggesting within-group synchronization.

Our results reveal a wide variability in proportion of breeding females, ranging from 29% to 81%, which is consistent with findings by Massei et al., (1996) and Fernández-Llario & Carranza (2000), who reported similar results, being the reproduction parameter showing a greater variability in Mediterranean wild boar populations. The mean number of corpora lutea per female was 4.5, being relatively stable across the 3 years studied with a range from 4.3 to 4.7, similar to that recorded in other Mediterranean regions (Brogi et al., 2022; Fernández-Llario & Carranza, 2000; Rosell et al., 2012b), but lower than that reported for northern latitudes which usually range from 5 to 7 corpora lutea per female (Abaigar, 1992; Ditchkoff et al., 2012; Malmsten et al., 2017). A similar pattern was found in litter size, as the mean litter size observed in our study was 3.9, ranging from 3.6 to 4.1 fetuses per female and not showing significant differences between years. This reveals a relatively low productivity compared to Northern countries with average adult litter sizes being around 6 fetus per female (Bywater et al., 2010). Mean intrauterine mortality rate was 16%, with only one site showing significant differences across years, in agreement with the findings of Cachelou (2021), who also reported stable mortality rates across different sites and years. Female body weight was a consistent and significant positive predictor of reproductive success across all models. Heavier females exhibited higher fertility (measured by the number of corpora lutea), larger litter sizes and higher breeding probability. This confirms the findings of previous studies suggesting that body condition is a critical determinant of reproductive output in many large mammal species, including wild boar (Albon et al., 1983; Canu et al., 2015; McCullough, 1999; Servanty et al., 2009). Nevertheless, no effect was detected on intrauterine mortality.

To assess the density-dependent effects on reproductive parameters, we analysed the relationship between population density and breeding probability, number of corpora lutea, litter size and intrauterine mortality. Our results showed that higher densities are associated with lower proportion of breeding females. This effect was observed not only for the current year's population density but also for the density recorded in the previous year, highlighting the potential lagged influence of density on reproductive outcomes. To our knowledge the effects of density on females breeding probability have not been described for wild boar before. Interestingly, breeding probability was the only reproductive parameter directly affected by density. This finding suggests that the primary reproductive adjustment to varying population densities lies in whether or not a female becomes pregnant, rather than the number of offspring produced. Similarly, Fernández-Llario (2000), found that the 'decision' breeding or not was the main adjustment of reproductive effort under drought conditions.

Density-dependent effects on reproduction have been more extensively studied in other ungulates. Albon et al. (1983) highlighted a density-dependent relationship with fertility and body weight in female red deer (*Cervus elaphus*). Similarly, Stewart et al. (2005) demonstrated that higher population densities negatively impacted body condition and proportion of breeding females in North American elk (*Cervus canadensis*). In Soay sheep (*Ovis aries*), density-dependent factors reduced fecundity, particularly in young and first-time breeders, and high densities were associated with lower twinning rates in adults. In saiga antelope (*Saiga tatarica*), population density was linked to reduced fecundity, particularly through decreased twinning rates in adults (Coulson et al., 2000). Bonenfant et al. (2009) further synthesized empirical evidence across multiple large herbivores, demonstrating consistent density-dependent effects on reproduction, such as delayed age of primiparity, reduced proportion of breeding females, and lower juvenile survival under high-density conditions. Barasona et al. (2020) discussed how high piglet mortality at early ages might represent a disease-mediated density-dependent mechanism limiting wild boar population growth in semi-intensive management systems. Their findings suggest that environmental factors and population density can interact in complex ways, affecting reproductive success and population dynamics.

In wild boar, previous studies have highlighted that population density may influence female body weight, reproductive success, and ultimately population growth (Bruinderink and Hazebroek, 1995; Imperio et al., 2012; Vetter et al.,

2015). However, other research has not detected any density-dependent effects on population growth, fertility, or litter size in wild boar (Choquenot, 1998; Frauendorf et al., 2016; Ditchkoff et al., 2012). Many of these studies are limited by short-term datasets or comparisons conducted within a single year at one or few sites.

After we detected density-dependence in breeding probability, we explored the mechanisms that drive this effect. The path model based on the three-year dataset shows a direct effect of density on breeding probability, but, contrary to our expectations, it does not show any effect through female body weight. However, when analysing a broader 23-year long-term dataset from the same region, we did detect a significant negative association between density and female body weight. The significant negative effect of current population density on body weight suggests that as density increases, females tend to weigh less, potentially due to resource limitations and heightened competition (Frauendorf et al., 2016; Barasona et al., 2020). In other ungulate species, as roe deer, population density has been described as a body size regulator, with higher densities being associated with smaller individuals, in response to stronger competition for food resources (Albon et al., 1983; Festa-Bianchet et al., 1998; Morellet et al., 2007).

Our results suggest that density-dependent reductions in breeding probability are mediated by body condition but also may occur through other mechanisms such as increased stress or social competition, which may impair reproductive success without significantly affecting body mass. The results also highlight the importance of long-term datasets for detecting density-dependent effects. In the three-year dataset, temporal or spatial variability may have masked the effect of density on body weight, or the statistical power may have been insufficient to detect subtle effects. In contrast, the 23-year dataset spanning 20 sites captured a wider range of density fluctuations, allowing for the detection of the density-body weight relationship.

The results of this study imply that high densities may limit population growth by reducing the number of pregnant females. However, as evidenced by the continuous population increases observed across Europe and worldwide, this mechanism alone is insufficient for effective self-regulation. The widespread availability of anthropogenic food resources can weaken natural regulatory processes, which may only show noticeable effects under extreme conditions of resource scarcity, such as severe droughts.

These findings highlight the need for management strategies that go beyond density reduction alone. Given the role of anthropogenic food resources in sustaining high wild boar populations, effective management should also focus on limiting access to human-derived food sources, such as agricultural crops, urban waste, and supplementary feeding. Additionally, adaptive management approaches that integrate population monitoring with habitat and resource availability assessments will be essential to anticipate population responses and mitigate human - conflicts.

4.1 Conclusions

Overall, our study contributes to the understanding of density dependence in wild boar reproduction, revealing two distinct mechanisms. The first is an indirect effect mediated by female body condition, where increased population density leads to heightened competition for resources, resulting in poorer body condition and lower breeding probability. The second mechanism involves a direct effect of density on breeding probability, independent of body condition. This effect is likely influenced by changes in social structure, home range dynamics, behaviour, stress levels, or disease transmission. The exact mechanisms behind this direct effect remain unclear and require further investigation to fully understand their role in wild boar reproduction and population dynamics.

Other reproductive parameters such as fertility rate, litter size, and intrauterine mortality are not influenced by density, suggesting that the primary response to changes in density is related to the likelihood of pregnancy rather than the number of offspring produced.

Our findings show the complexity of wild boar population dynamics, where high densities can reduce breeding success, limiting population growth. However, this mechanism alone is insufficient for self-regulation. By understanding how density influences breeding probability and population growth, managers can develop more precise and effective control strategies. Moreover, adaptive management, which includes continuous population monitoring, forecast of population trends, adjustable population control strategies and limiting access to anthropogenic food, is essential for anticipating population changes and mitigating conflicts with human activities.

Our findings show the complexity of wild boar population dynamics, where high densities may reduce breeding success, thereby limiting population growth.

However, this mechanism alone is insufficient for self-regulation. Understanding how density impacts breeding probability and population growth allows managers to design more targeted and informed control strategies. In addition, adaptive management—incorporating continuous population monitoring, forecasting population trends, flexible control measures, and restricting access to anthropogenic food sources—will be critical for anticipating population changes and minimizing human-wildlife conflicts.

5 Author contributions

J. Colomer: Writing – original draft, Methodology, Formal analysis, Data curation, Conceptualization. G. Massei: Writing – review & editing, Supervision, Conceptualization. C. Rosell: Writing – review & editing, Funding acquisition, Conceptualization. J.D. Rodríguez-Teijeiro: Writing – review & editing, Supervision, Methodology.

6 Acknowledgements

This research is based on samples collected with the support of the Catalan Government, particularly through the collaboration of Yolanda, Josep Queixans, Joan Olivella, and Juan Fernández. We also utilized data from the Catalan Wild Boar Monitoring Program, funded by the Catalan Government, the Barcelona Regional Council (Diputació de Barcelona), the Zona Volcànica de la Garrotxa Natural Park, and the Gavarres Consortium. Special thanks to the hunting teams, technicians, rangers and site coordinators that collaborate with the data collection and management. We also thank Mariàngels López for her huge contribution to sample analysis in the laboratory, and to Anna Colomer for her assistance in data organization. To Stefano Focardi for a short but extremely useful discussion.

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Chapter 3.

'Reserve effect': An opportunity to mitigate human-wild boar conflicts

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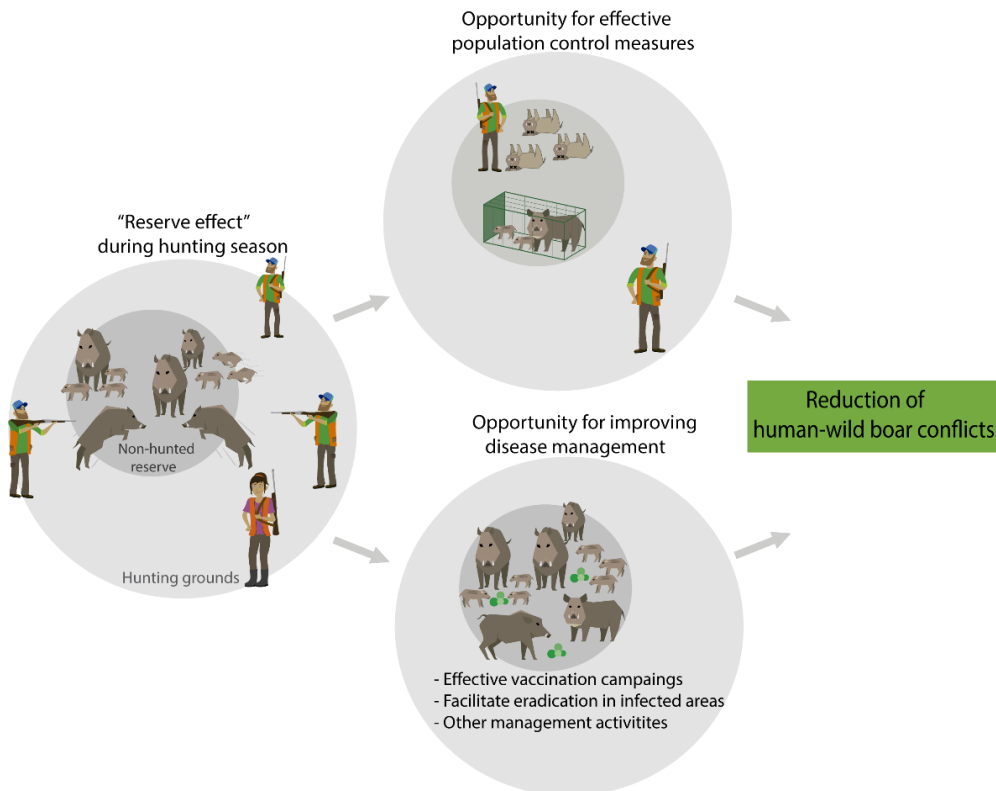
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Published in: Colomer, J., Rosell, C., Rodríguez-Teijeiro, J.D. & Massei, G. 2021.
'Reserve effect': An opportunity to mitigate human-wild boar conflicts. *Science of The Total Environment*, 795,148721. ISSN 0048-9697.
<https://doi.org/10.1016/j.scitotenv.2021.148721>

Highlights

- Wild boar impacts are growing, in parallel with the species' numbers and range.
- Camera traps showed wild boar congregate in reserves where hunting is banned.
- A drastic reduction of wild boar in reserves was observed after a single hunt.
- Population control and disease management can benefit from 'Reserve effect'.
- 'Reserve effect' offers opportunities to mitigate human-wild boar conflicts.

Graphical abstract



Keywords

Population control; Wild boar density; Camera traps; Conflict mitigation; Social Organization; Wildlife management

Abstract

Wild boar growth in numbers and range is associated with increasing economic and environmental impact. Hunting has been traditionally used to reduce wild boar numbers. Areas where hunting is not allowed may attract wild boar from neighbouring hunting grounds. This phenomenon is called 'reserve effect' and could cause temporarily localised, high densities of wild boar in areas where hunting is banned. To investigate the occurrence of 'reserve effect', this study was conducted in two natural reserves of 400 and 250 ha inside the Montseny Natural Park, Catalonia, Spain where regular hunting of wild boar is not permitted, and only sporadic driven hunts/year are authorised for population control. The aims of the study were to evaluate if wild boar use these reserves as a refuge when hunting is carried out in the surrounding areas and to assess the effects that occasional drive hunts inside these reserves may have on wild boar numbers and social organization. From 2012 to 2015 camera traps were placed in the two reserves without using any bait. Cameras operated for 1.759 days, including hunting and non-hunting seasons, and 37.574 wild boar images were obtained. A 'reserve effect' was detected, as following hunting in the surroundings grounds, the number of wild boar increases inside reserves. Occasional driven hunts conducted in the reserves are effective in reducing the number of individuals and the effects persist for at least 45 days. Hunting disrupts wild boar social organization, as group size was significantly reduced. These results suggested that targeting refuge areas, once hunting in the surroundings causes wild boar to concentrate in these areas, is effective for population control. These findings could also be used to design strategies to optimise population control and offer opportunities for disease management such as vaccination, or to facilitate eradication in areas affected by disease outbreaks.

1 Introduction

Wild boar occur in a wide range of habitats and climates, have few natural predators and are characterised by high reproductive rates. This has led to a fast populations growth that has increased in recent decades across Europe, resulting in high population densities in many countries (Bieber & Ruf, 2005; ENETWILD consortium, 2019a; Massei et al., 2015; Náhlik & Sándor, 2003; Sáez-Royuela & Tellería, 1986) and causing a wide range of conflicts with conservation and human activities.

This species has significant economic and environmental impacts such as damages to crops, urban areas and infrastructures (Cai et al., 2008; Ficetola et al., 2014; González-Crespo et al., 2018; Ikeda et al., 2019; Schley & Roper, 2003) and reduction of biodiversity richness and species abundance (Bongi et al., 2017; Calevo et al., 2017; Carpio et al., 2016; P. Genov & Massei, 2004; Herrero et al., 2005). Wild boar also poses threats to public health and livestock, due to traffic accidents and to transmission of diseases, such as African swine fever (ASF), classical swine fever and foot and mouth disease (González-Barrio et al., 2015; Guberti et al., 2019; Rossi et al., 2015; Sáenz-De-Santa-María & Tellería, 2015). All these impacts have important economic implications as the costs derived from traffic accidents, crop and urban areas damages and the consequences of disease outbreaks can amount to billions of euros (Barrios-Garcia & Ballarí, 2012; Forman et al., 2009; Guo et al., 2016; Halasa, Bøtner, et al., 2016).

To mitigate these impacts, wild boar population control is required and supported by wildlife managers, landowners, farmers, and public administrations including health services. Population control is carried out mainly by recreational hunting (e.g., driven hunts, solo hunts, etc.) and to a much lesser extent by trapping. Understanding the factors affecting the species' behavioural response to hunting is crucial to apply effective and evidence-based population control. In most countries, hunting is the main cause of wild boar mortality (Keuling et al., 2013; Massei et al., 1997b, 2015; Nores et al., 2008; Toïgo et al., 2008; Virgós, 2002). Hunting affects population size but may also influence spatial, social and temporal behaviour, and in particular home ranges size, habitat use, activity patterns and group composition (Baubet et al., 1998; Keuling et al., 2008; Maillard & Fournier, 2014; Scillitani et al., 2010; Thurfjell et al., 2013; Vassant et al., 1988). When driven hunts are carried out, neighbouring areas where hunting is not allowed may be used as a refuge by wild boar. This

phenomenon, known as 'reserve effect' has been described in previous studies (Frank et al., 2015; Grignolio et al., 2011b; Sodeikat & Pohlmeier, 2003b; Tolon & Baubet, 2010). Understanding how wild boar use these reserves is essential to optimise population control and disease management strategies, particularly when the latter are based on a mosaic of areas where culling may or may not be allowed (Keuling et al., 2018; Tolon et al., 2009). Furthermore, no studies have addressed the impact of driven hunts on wild boar behaviour and numbers inside reserves adjacent to areas where hunting occurs. This is particularly relevant for management of diseases such as ASF that rely on core and buffer zones around the outbreak where culling is temporarily banned, and on an intensive hunting area, surrounding the buffer zone, where culling is encouraged (Jori et al., 2020; More et al., 2018).

As wild boar impact is often associated with local population density, the effectiveness of interventions employed to reduce such densities is based on estimating the number of animals before and after population control has been implemented. Of the methods available to estimate wild boar population density, several require significant resources, making their implementation unfeasible. One of the most widespread methods is based on hunting statistics, which allows monitoring of large areas with reasonable costs and staff time (ENETWILD consortium, 2019b; Gamelon et al., 2012). Camera traps can also be used to obtain consistent estimates of populations size (Chauvenet et al., 2017; Keuling et al., 2018; Massei et al., 2017; Minuartia, 2020; Rowcliffe et al., 2008). Moreover, camera trap images allow to collect data on individual behaviour, social interactions, group composition, reproductive output, activity patterns and responses to human presence and hunting (Erdtmann & Keuling, 2020; Lashley et al., 2018; Oliveira-Santos et al., 2013; Palencia et al., 2019; Rowcliffe et al., 2014, 2016). This study used camera traps to monitor changes in wild boar numbers, group size and composition before and after hunting occurred.

The aims of the study were 1. to evaluate if wild boar use reserves as a refuge when hunting is carried out in the surrounding areas; 2. to assess the effects that occasional drive hunts inside these reserve have on wild boar numbers; and 3. to determine the effects of hunting on wild boar group size and composition. The hypotheses were that i) following hunting in the surroundings grounds, the number of wild boar increases inside these reserves; ii) occasional driven hunts conducted in the reserves are effective in reducing the number of individuals and iii) hunting disrupts wild boar social organization.

2 Materials and methods

2.1 Study area

The study was carried out in the Montseny natural park which covers 31.064 ha and is situated in the Catalan pre-littoral mountain range (NE Spain) 17 km from the coastline, with an altitude ranging from 100 to 1.700 m a.s.l. (Figure 4.12). The area is located in the Mediterranean region but at the higher altitudes above 1.000m, the climate is temperate, creating a marked gradient of climate and vegetation. Average annual rainfall is 1.053 mm. Mean annual temperature at the highest altitudes is 7.1°C with a maximum monthly mean in July of 15.5°C and a minimum in January of 1.0°C. At lower altitudes, mean annual temperature is 14.8°C with a monthly mean maximum in July of 23.6oC and a minimum on January with 7.2oC (Servei Meteorològic de Catalunya, 2016).

Inside the natural park, there are eight areas with special protection known as natural reserve areas (here after NRA), with occupying a total of 2,606 ha (8.4% of the total surface of the natural park) where regular hunting is not permitted. This study was carried out in the two largest areas: Matagalls-Sant Marçal-Vall de Riudeteix (hereafter referred as Riudeteix) and Vallforneres, which together occupy 1,515 ha.

Riudeteix is situated between 670 and 1.697 m a.s.l and includes an area of 1.117 ha. The vegetation is composed mainly by dense forests dominated by holm oak (*Quercus ilex*) forest, intermixed with beech (*Fagus sylvatica*) and chestnut (*Castanea sativa*) forests. At higher altitudes, the vegetation is dominated by bushes such as junipers (*Juniperus communis ssp. nana*) and broom (*Genista purgans*), mesophilic and xerophilous meadows, wet meadows and reedbeds (OTPAT, 2008).

Vallforneres includes an area of 389 ha with a high diversity of habitats situated between 700 and 1.300 m a.s.l. The vegetation is dominated by sclerophyllous species, mainly holm oak, but also conifers and riparian forest, and at the higher altitudes, open habitats dominated by grassland and shrubs as in Riudeteix.

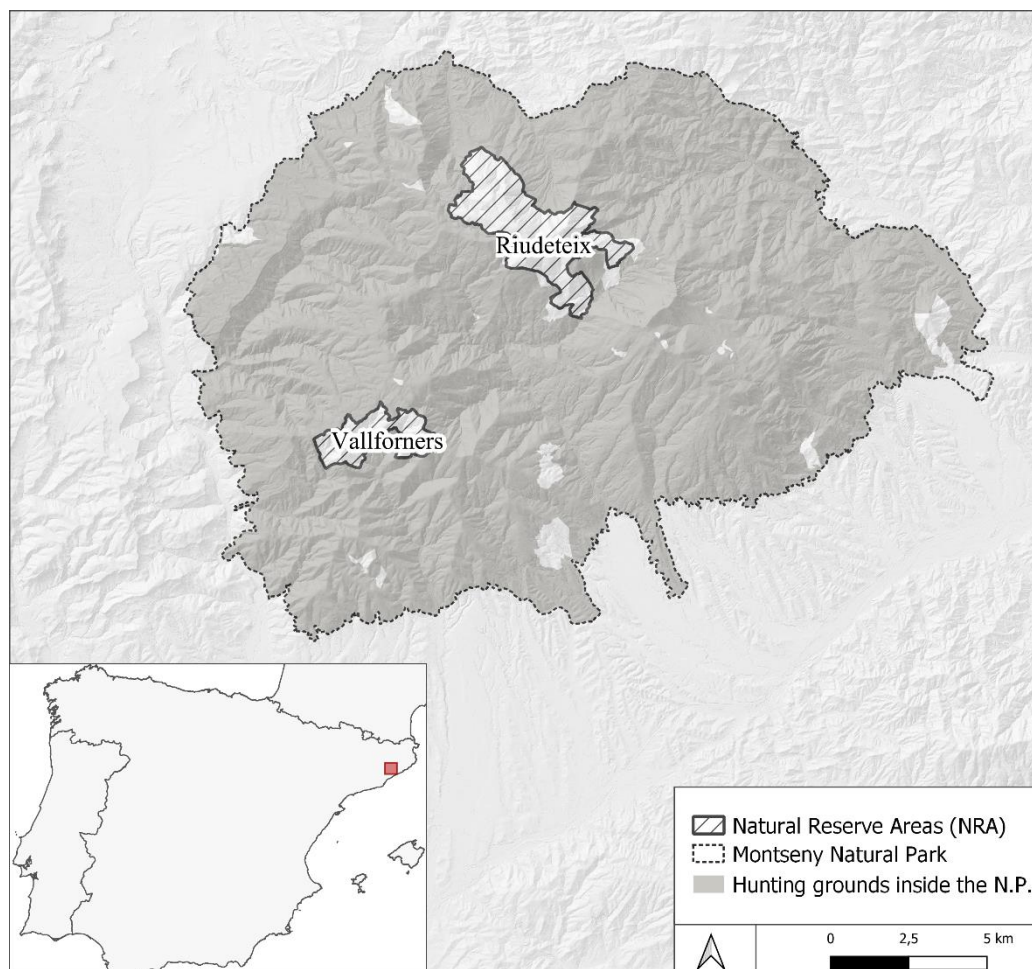


Figure 4.12. Location of the two study sites, the Natural Reserve Areas (NRA) of Vallforners and Riudeteix situated within the Montseny natural park, Catalonia, Spain. Hunting areas occupy almost the whole area of the natural park except the NRA and other small sites.

2.2 Hunting data – Wild Boar Monitoring Program

In Catalonia a wild boar monitoring program was implemented in 1998, based on data provided by hunting teams at the end of the hunting seasons. Participants deliver a notebook where data from each driven hunt are recorded and include date, number of hunters and dogs, number of wild boar hunted, and number of animals observed but not hunted. These data are used to estimate wild boar density in each of the 22 participant areas in Catalonia. Currently more than 173 hunting groups participate in the program, providing information on about 5.000 hunts each year. The complete database contains data about more than 85.000 driven hunts. These data are analysed to monitor population trends across the whole region, with reports annually published by the Catalan Ministry

of Agriculture, Livestock, Fisheries and Food since 1998 (DARP (Departament d'Agricultura Ramaderia Pesca i Alimentació), 2020). Since 1998, Montseny natural park participates to the Catalan Wild boar Monitoring Program.

Two wild boar density indices are calculated each year: 1. a relative density index (Rosell, 1998) which takes into account the total number of wild boar harvested, the hunting effort and the surface of the hunting area and 2. an estimate of the absolute density (Sáez-Royuela & Telleria, 1987), considering the ratio of wild boar hunted vs. observed per area (Table 4.8). These methods are often used for monitoring wild boar trends (Gamelon et al., 2012; Keuling et al., 2018; Massei et al., 2015). Moreover, recent comparison with other density estimation methods based on camera trap, such as the Random Encounter Model (Chauvenet et al., 2017; Rowcliffe et al., 2008) carried out in the Montseny natural park, have provided similar density estimations (Minuartia, 2020), reinforcing the field operatives' confidence in the method based on hunting data.

During the study period (2012 to 2015) wild boar density estimate by the wild boar monitoring program in Montseny natural park increased from 10 individuals/km² in 2012/2013 to 16 individuals/km² in 2015/2016 (Table 4.8), the maximum ever registered in the 20 years monitoring period (DARP-Departament d'Agricultura Ramaderia Pesca i Alimentació, 2016).

Throughout the whole natural park, surrounding the two NRA, there was a relatively high hunting pressure during the study periods according to the monitoring program, as on average 110 hunts (SE=0.95) were carried out each month (from September to February), representing around 1.4 hunts/km². Hunts had a mean participation of 24 (SE=0.44) hunters and 19 (SE=0.37) dogs (Table 4.8).

Population control driven hunts were exceptional hunts carried out inside the NRA. These were authorised by the natural park authorities with the objective of culling the maximum number of wild boar inside these areas. These control driven hunts carried out once or twice per year, during the winter months, attracted a higher number of participants, with an average of 31 (SE=0.58) hunters and 27 dogs (SE=0.49), compared to regular driven hunts carried out in the surroundings areas.

Table 4.8. Wild boar density estimates and hunting pressure parameters in the Montseny Natural Park during the study period. Data from the Catalan Wild Boar Monitoring Program (DARP, 2016).

variable	2012/2013	2013/2014	2014/2015	2015/2016
Wild boar density (individuals/km ²)	10.29	11.59	11.31	16.34
Number of hunts/year/km ²	1.40	1.37	1.33	1.54
Mean number of hunts/month	110.16	107.33	104.00	117.17
±SE	7.10	6.20	5.20	4.12
Mean number of hunters/hunt	23.14	23.61	24.10	24.05
±SE	0.43	0.45	0.45	0.39
Mean number of dogs/hunt	18.79	18.94	18.21	18.02
±SE	0.37	0.40	0.36	0.32

2.3 Data collection

Camera trapping was conducted to monitor abundance and group composition of wild boar inside the two reserves. No bait was used to attract the animals. Reconyx RC55 and HC500 camera traps were situated in trees next to active wild boar trails.

Five camera trap locations (two in Riudeteix and three in Vallforners respectively) were in operation during the whole period and were considered for the analysis. Camera traps operated for 1,759 days (Table 4.9). Other cameras were placed in the NRA during these years but were not working for the whole period and have not been included in the present study. Nevertheless, the data provided by these extra cameras has been used to check consistency of the results obtained. The same patterns of numbers of individuals inside the reserve are during the hunting and non-hunting season were coincident with the ones observed in the cameras selected for this study. Moreover, the fact that the results obtained in the present paper by the 5 cameras are consistent across the four years of study, together with the high number of day in operation and registers obtained, reinforce the robustness of the dataset and the conclusions that can be drawn.

In Riudeteix two camera traps were placed in an area of 250 ha situated between 875 and 1050 m a.s.l., covered mainly with Mediterranean oak and excluding the higher open areas of the NRA. In Vallforners three camera traps were distributed across the whole area of the NRA, dominated by Mediterranean oak. Cameras were placed in locations without attractive resources for wild boar, in points with conditions and habitats similar to the whole study area. Locations were chosen

to assure that camera traps had a good area of vision of wild boar movements, avoiding areas with dense vegetation that interfere in the camera traps range.

Table 4.9. Duration of the camera trap monitoring in each NRA during both open hunting season (September to February) and closed hunting season (February to September) in the surrounding areas of the Montseny Natural Park. Two and three camera traps were used in Riudeteix and Vallforners respectively.

Natural Reserve Area	Hunting season	Installation	Removal	Proportion of days in operation
Riudeteix	Hunting 2012/2013	30/10/2012	12/03/2013	82%
	Hunting 2013/2014	06/11/2013	23/02/2014	100%
	Non-hunting 2014	24/02/2014	06/09/2014	100%
	Hunting 2014/2015	07/09/2014	22/02/2015	100%
	Non-hunting 2015	23/02/2015	06/09/2015	99%
	Hunting 2015/2016	06/09/2015	18/02/2016	100%
	Total			97%
Vallforners	Hunting 2012/2013	-	-	
	Hunting 2013/2014	03/10/2013	23/02/2014	81%
	Non-hunting 2014	24/02/2014	31/08/2014	100%
	Hunting 2014/2015	01/09/2014	22/02/2015	76%
	Non-hunting 2015	23/02/2015	05/09/2015	100%
	Hunting 2015/2016	06/09/2015	18/02/2016	100%
	Total			92%

2.4 Data analysis

Visual identification was used to define the minimum number of individuals, the age class and group size for each group of wild boar that visited the camera traps. Photographs taken less than 10 minutes apart were considered the same visit (Massei et al., 2017). Group composition was classified in four categories, matriarchal groups, solitary males, subadults or indeterminate; group size was determined by counting the total number of individuals in each group. Matriarchal groups were described as any group of one or more adult sows with their youngs. Subadult groups are composed by small number of subadults. Camera traps recorded a sequence of 5 consecutive photos and the minimum time lag between bursts was selected (0.6 seconds). For each sampling location, the daily mean number of wild boar (minimum count of individuals recorded in the photos taken per day in each camera trap) was calculated. Before any analysis, the autocorrelation between the daily individual counts was tested indicating that each daily observation was independent from the previous and following days.

2.4.1 'Reserve effect' analysis

To investigate the 'reserve effect', camera traps were used to assess the presence of wild boar inside the reserve areas. The study periods of 2014/2015 and 2015/2016 were selected, since they are the years that present complete camera trap data for the regular hunting and no hunting seasons. The number of wild boar individuals recorded by the camera traps inside the NRA (where hunting is normally forbidden) during regular hunting and non-hunting season in the surroundings areas was analysed. Differences of this variable in each site and season between hunting and non-hunting periods, and before and after the population control hunt, were tested using Mann-Whitney tests. Sequential Bonferroni corrections (Rice 1989), in which alpha was 0.05 (number of years by NRA) were used for the first comparison. Differences in group composition before and after the regular hunting season and before and after the population control driven hunt were tested by chi-square tests. Only the period before the first population control driven hunt inside the NRA was considered, as after the disturbance the NRA could not be considered a hunting reserve anymore.

2.4.2 Population control driven hunt inside the reserves

For testing the effects of the population control driven hunt inside the reserves on wild boar numbers and group composition camera traps were used to assess the number of individuals before and after the hunts. The four study periods in which the camera traps were in operation during the hunting season were considered (2012/2013, 2013/2014, 2014/2015 and 2015/2016). An analysis before / after the hunting control within the reserve was carried out to assess the effect of hunting on numbers and group composition. A period of 45 days after the first population control driven hunt was considered, as previous studies reported that the effects of a driven hunt on wild boar home ranges can be detected during a period of 4 to 6 weeks (Sodeikat & Pohlmeier, 2003b). In addition, the present study also tested whether the effects of the population control driven hunt on wild boar numbers and group composition persisted for longer periods, specifically for 60 days, in the instances where data were available.

To evaluate the effectiveness of the population control hunt in decreasing the number of wild boar inside the NRAs, an Interrupted time series analysis (ITS) was carried out. The ITS examined changes in the slope of the trend of daily mean number of wild boar detected/camera trap/day in each study site during

the hunting season in Montseny natural park before and after the population control hunts were carried out inside the reserves (Bernal et al., 2017). Before the ITS analysis was carried out, data autocorrelation (tendency of observations closer in time to be more similar between each other) and overdispersion (variability greater than the expected by the model) were tested. As the data did not show autocorrelation but tested positive for overdispersion, a Quasi-poisson distribution was used, which allows the variance to be proportional rather than equal to the mean. The ITS analyses were carried out using the script available on (Bernal et al., 2017). All data analyses were carried out in R (R Core Team, 2020).

3 Results

3.1 'Reserve effect'

During 2014/2015 and 2015/2016 seasons, camera traps were in operation for 723 and 724 days respectively (Table 4.9) and recorded 7,800 and 12,908 wild boar images in Riudeteix and Vallforneres respectively. Wild boar were detected in all operational camera traps, with an average daily number across sites and seasons of 2.45 (SE=0.11, range= 0-41) wild boar /day.

Comparison of the number of individuals between regular hunting and non-hunting season, showed that wild boar concentrate in the NRA when hunting occurs in the surroundings areas. The average number of individuals was significantly higher inside the NRA during the hunting season, than the non-hunting season for both years in the Vallforneres site (2014/2015: Mann-Whitney U-test $W=4785.5$, $n_1=195$, $n_2=85$, $P<0.001$; 2015/2016: $W=7732$, $n_1=193$, $n_2=91$, $P<0.001$) and for the 2015/2016 period in the Riudeteix site (U-test $W=6815$, $n_1=194$, $n_2=82$, $P<0.001$), but not for Riudeteix during 2014/2015 ($W = 12962$, $n_1=195$, $n_2=131$, $P= 0.811$) (Figure 4.13).

For both study sites, the mean group size detected inside the NRA was higher during the regular hunting season than the non-hunting season for both years in the Vallforneres site (2014/2015: Mann-Whitney U-test, $W=3712$, $n_1=287$, $n_2=151$, $P<0.001$; 2015/2016: U-test, $W=31775$, $n_1=171$, $n_2=185$, $P<0.001$) and for 2015/2016 in the Riudeteix site (U-test, $W=5715.5$, $n_1=163$, $n_2=162$, $P<0.001$) but not for Riudeteix during 2014/2015 ($W = 21168$, $n_1=207$, $n_2=151$, $p\text{-value} = 0.576$). Mean group size for each period are reported in supplementary materials (Table S1).

Group composition differed between the non-hunting and the regular hunting season for both sites and study periods after Bonferroni correction (Vallforners: 2014/2015: $X^2_3=42.90$, $P<0.001$; 2015/2016: $X^2_3=55.71$, $P<0.001$. Riudeteix: 2014/2015: $X^2_3=32.04$, $P<0.001$; 2015/2016: $X^2_3=23.09$, $P<0.001$). The proportion of matriarchal groups was higher inside the NRAs during the hunting season than during the non-hunting season in all cases. No consistent patterns were observed on proportions of solitary males and subadults across years and sites (Figure 4.14).

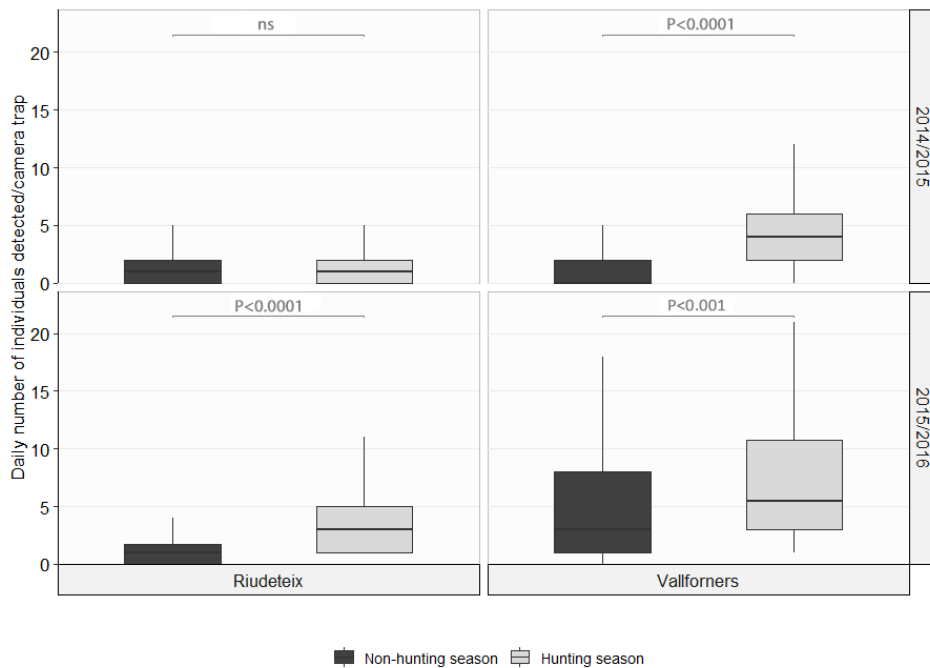


Figure 4.13. Daily number of wild boar individuals detected / camera trap inside the NRAs during non-hunting season (spring and summer) and hunting season (autumn and winter) in the Montseny natural park before any population control hunt was carried out inside the NRAs. The line inside the box represents the median, lower and upper box boundaries represent 25th and 75th percentiles respectively and lower and upper error lines; 10th and 90th percentiles respectively. ns: $p > 0.05$.

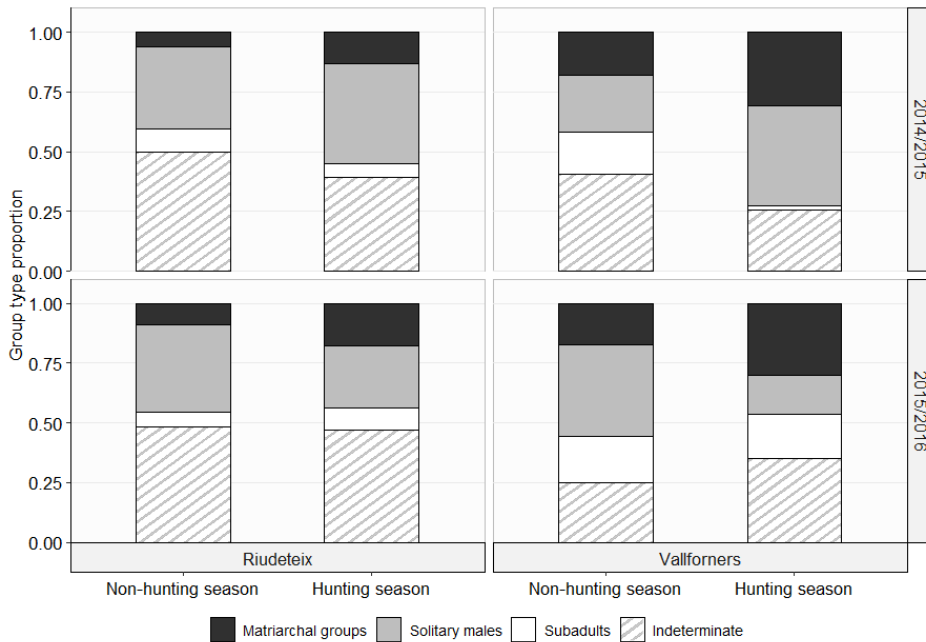


Figure 4.14. Group composition proportions observed in the two non-hunted study sites during non-hunting and hunting season in the other hunted parts of the Montseny natural park.

3.2 Effects of population control driven hunt inside the reserves

During the hunting seasons from 2012/2013 to 2015/2016, two and three camera traps were in operation for 1,102 days (Table 4.9) and recorded 17,532 and 20,042 wild boar images in Riudeteix and Vallforners respectively. Wild boar was detected in all operational camera traps, with an average daily number of individuals across sites and seasons of 2.75 (SE=0.10, range= 0-41).

The population control driven hunts inside the reserve were carried out once per season except for Vallforners in 2014/2015 and 2015/2016, when two population control hunts were carried out but only the period after the first hunt has been considered for the analysis.

The mean number of wild boar detected/camera trap for a period of 45 days after the population control hunt was lower than that before the hunt for all years in Vallforners (2013/2014: Mann-Whitney U test , $W=278$, $n_1=105$, $n_2=45$, $P=0.001$; 2014/2015: $W=501.1$, $n_1=30$, $n_2=45$, $P<0.001$, 2015/2016: $W=427.5$, $n_1=91$, $n_2=45$, $P=0.019$) and for the first three years in Riudeteix (2012/2013: $W=532.5$, $n_1=53$, $n_2=45$, $P<0.001$; 2013/2014: $W=488$, $n_1=152$, $n_2=34$, $P<0.001$; 2014/2015: $W=1501$, $n_1=131$, $n_2=42$, $P<0.001$). Only the 2015/2016 season in Riudeteix the decrease was not significant ($W=287.5.5$, $n_1=67$, $n_2=45$, $P=0.079$) (Figure 4.15). Data of 60 days after the hunt were only available in four cases

(Riudeteix 2012/2013 and 2015/2016 and Vallforners 2014/2015 and 2015/2016). In these cases, differences in wild boar numbers before and after the population control driven hunt were significant only in Riudeteix for the season 2012/2013 (Mann-Whitney U test, $W=651$, $n_1=53$, $n_2=60$, $P<0.001$), in all other cases (Riudeteix 2014/2015, and Vallforners 2014/2015 and 2015/2016) differences were not significant (Mann-Whitney U test, $W<800$, $P>0.049$).

The interrupted time series analysis showed that the population control driven hunts inside the reserves reduced wild boar numbers and that the effects were still lasting after 45 days (Figure 4.16). In all study periods for both sites, the observed trend based on the regression model of individual numbers detected per day was lower than the predicted trend if the intervention had not been carried out.

The effect of single population control driven hunts inside the reserves on group size was not consistent across areas and years (Table S2). At Vallforners, there was a significant decrease in mean group size for all the three seasons (2013/2014: Mann-Whitney U test: $W=35355$, $n_1=285$, $n_2=181$, $P<0.001$; 2014/2015: $W=54655$, $n_1=162$, $n_2=208$, $P<0.001$, 2015/2016: $W=42640$, $n_1=153$, $n_2=214$, $P<0.001$). At Riudeteix, mean group size differed for the 2015/2016 season ($W=6694$, $n_1=109$, $n_2=85$, $P<0.001$) but not for the first three seasons ($W<22066$, $P>0.164$), although the same trend in decreased group size was observed.

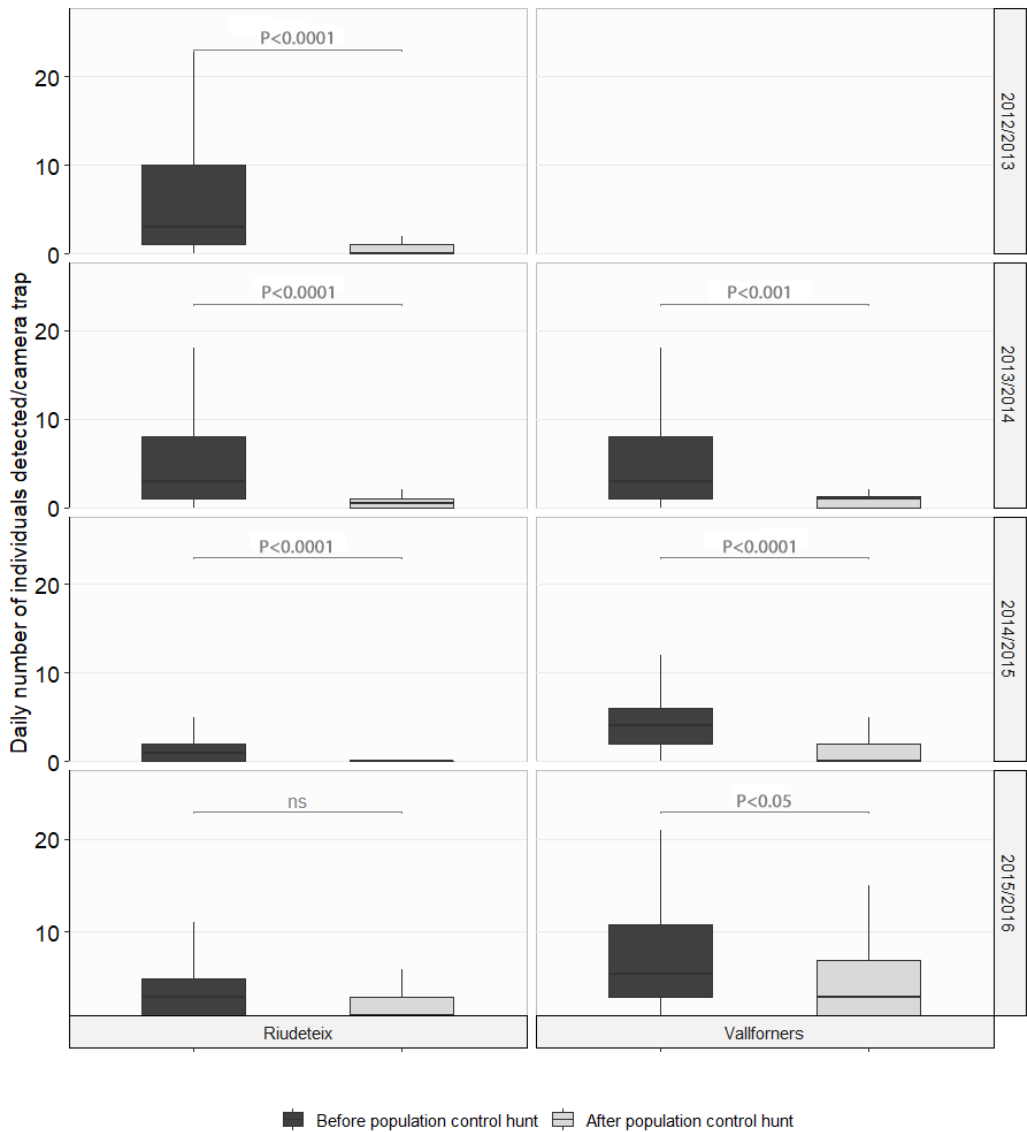


Figure 4.15. Daily number of wild boar detected/camera trap during the hunting season in Montseny natural park before and 45 days after the population control hunts in each site and study period. The line inside box represents the median, lower and upper box boundaries represent 25th and 75th percentiles respectively and lower and upper error lines; 10th and 90th percentiles respectively. ns: $p > 0.05$.

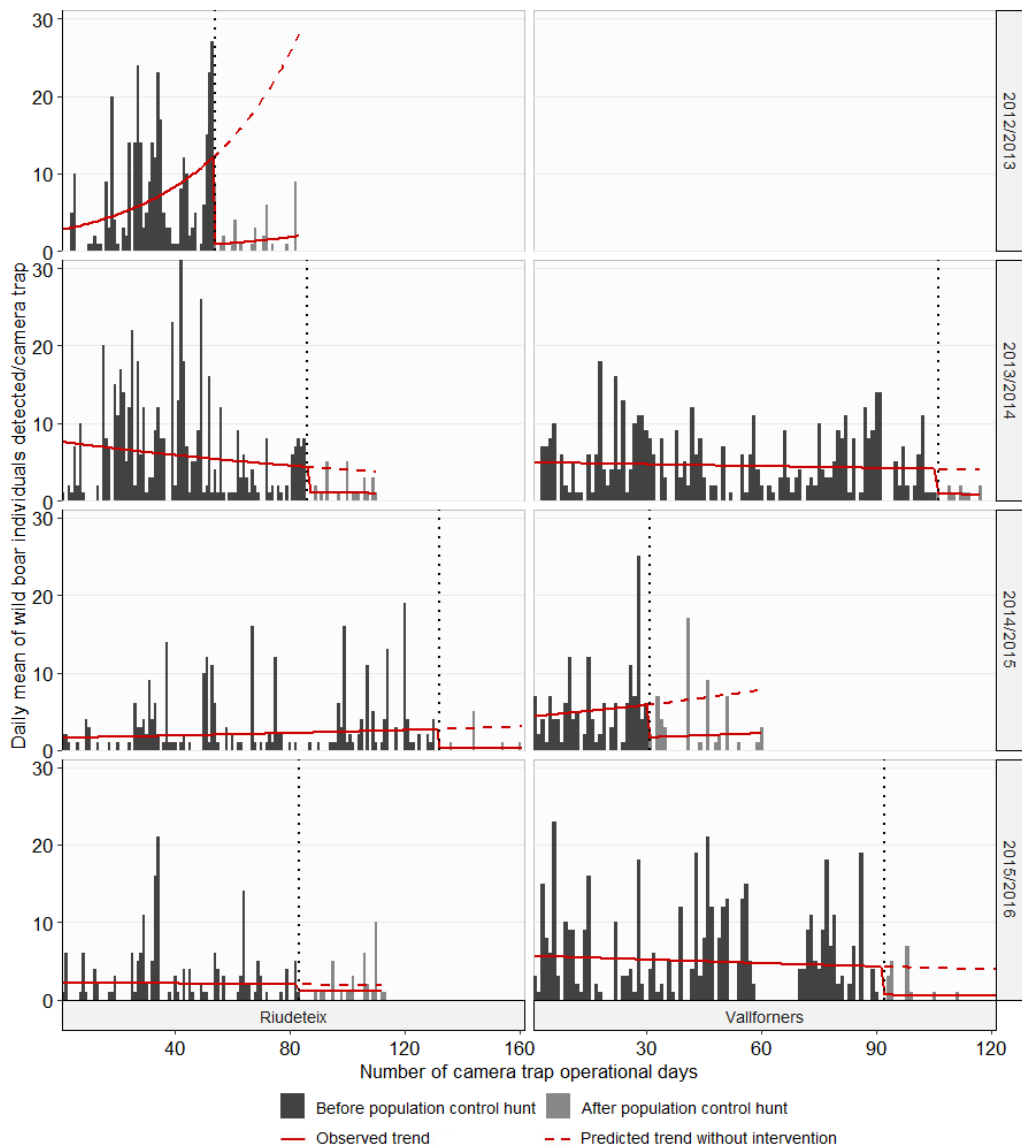


Figure 4.16. Daily mean number of wild boar detected/camera traps in each site and study period during the hunting season in Montseny natural park before and after the population control hunts (represented by vertical black dotted lines) were carried out inside the reserves. Solid lines show the actual trend before and after the driven hunt. Dashed lines show the predicted trend based on regression model if the population control hunt had not been carried out. The 'after' period includes 45 days after the population control hunt.

Where individual and groups could be identified, consistent but only borderline significant differences in group composition frequencies emerged when comparing the period before the population control driven hunt and the 45 days after the hunt (Figure 4.17). No differences were observed in Vallforners (after Bonferroni correction) for all three study periods (2013/2014: $X^2_3 = 9.11$, $P = 0.028$;

2014/2015: $X^2_3=10.56$, $P=0.032$; 2015/2016: $X^2_3=6.52$, $P=0.030$) and in Riudeteix only 2015/2016 ($X^2_3=17.98$, $P<0.001$) was significant after Bonferroni correction ($X^2_3<7.82$, $P>0.049$). Bonferroni correction is a very conservative test and in all cases the p values were very close to significance.

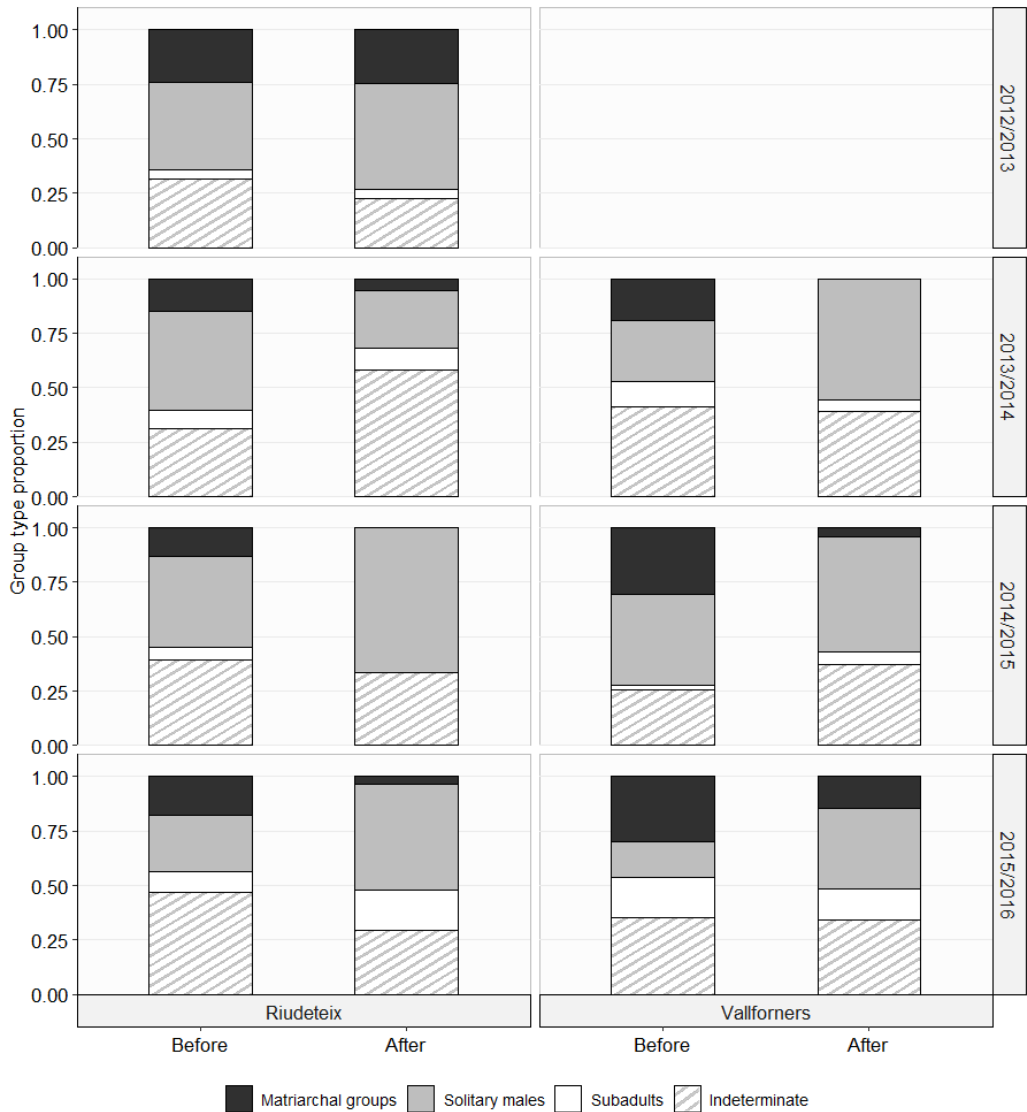


Figure 4.17. Group composition proportions observed in the two study sites before and after the population control hunts inside the reserves.

4 Discussion

This study substantiated the hypotheses that i) following hunting in the surroundings grounds, the number of wild boar increases inside reserves; ii) occasional driven hunts conducted in the reserves are effective in reducing the number of individuals; and iii) hunting disrupts wild boar social organization.

In particular, the study confirmed that when driven hunts, that involve tens of hunters and dogs, are carried out, wild boar seek refuge in reserve areas where hunting is banned. The results also indicated that this behaviour seems particularly apparent in matriarchal groups and that hunting affects group size and composition. This was also the first study that investigated the effects that control driven hunts inside refuge areas have on wild boar numbers and on group composition. Although few camera traps were employed during the study, albeit for consecutive years, the results were reasonably consistent across the two reserves and the years.

The 'reserve effect' for wild boar was detected in this study, similarly to what described in previous studies (Amici et al., 2012; Rosell et al., 2004; Tolon et al., 2009; Tolon & Baubet, 2010). Amici et al. (2012) found that the presence of non-hunted areas close to cultivated areas was a significant factor affecting crop damage by wild boar, supporting the hypothesis of a 'reserve effect'. Tolon et al. (2009) showed that wild boar moved to the reserve during the open hunting season but also that there was a threshold distance (2.1 km) beyond which animals did not respond to hunting disturbance as they might have not perceived the safety in the reserve. As the two reserves in the present study are more than 5 km apart, it is likely that the wild boar attracted to one of the reserves were not affected by the other one. Rosell et al. (2004) found the maximum number of wild boar in the non-hunted reserves in a wetland area during the autumn months, which coincided with the start of the hunting season in the surroundings. This also coincided with the lack of food resources in the neighbouring areas, which were occupied mainly by cereal crops harvested at the end of summer and might have encouraged wild boar towards the reserves where food resources are available during autumn and winter. The same study also observed larger group size during the mating season which coincided with the hunting season. The present study showed that group size and proportion of matriarchal groups increased significantly inside the reserves during the hunting season (autumn and winter). These variations could be due to both the

hunting pressure but also to seasonal variations in social organization at the beginning of the mating season as in (Rosell et al., 2004).

A 'reserve effect' has also been described for other ungulate species, for instance roe deer (*Capreolus capreolus*) sought refuge in protected areas when hunting with dogs was conducted in the surroundings, even though this species was not targeted by these hunts (Grignolio et al., 2011b). Similarly, farmland (Casas et al., 2009) and wetland birds species (Bregnballe & Madsen, 2004; Madsen, 1998) during the hunting season switch their resting areas to sites where hunting is banned.

Conversely, (Brogi et al., 2020) did not find any evidence of 'reserve effect' in wild boar and attributed the increased number of animals in a non-hunted areas during autumn to the presence of food resources inside these areas. In the present study, food resources appeared equally distributed as there is the same type of habitat, dominated by holm oak, intermixed with beech and chestnut forests inside and outside the reserves. The increase of wild boar numbers was very likely due to the safety that non-hunted areas offered during the hunting season, as partly indicated by the sudden shift in numbers once the hunting season had started.

Where the 'reserve effect' occurs, adaptive management is required to achieve population reduction objectives across a whole area. For this reason, one or two control driven hunts per year were authorized inside the NRAs in Montseny natural park where hunting is normally banned. This study confirmed the hypothesis that these occasional hunts are effective in decreasing number of wild boar in the reserves. The effect of these hunts persisted for at least 45 days, in agreement with previous studies that showed that after a single hunt wild boar returned to their original home ranges within four to six weeks (Sodeikat and Pohlmeier, 2002). The reduced numbers of wild boar inside the reserves post-occasional driven hunts could be due to a combination of individuals that have been culled and animals that emigrated outside the reserves. Spatio-temporal variations of risk perception are major drivers of animal distribution especially for intensely preyed upon or harvested species responding to the so called "landscape of fear" (Brown et al., 1999; Thurfjell et al., 2013; Tolon et al., 2009). Future studies using camera traps inside and outside the reserves to estimate wild boar numbers throughout the year should establish whether the persistent decreased number of wild boar inside the reserves, following a single hunting event, is due to numbers removed by hunters, to emigration or to both.

The results show that single driven hunts carried out inside the reserves resulted in a decrease of group size. This may be caused by loss of individuals that have been culled but also from group disruption or individuals leaving the original groups. Previous studies found that hunting, even a single driven hunt affects social behaviour, activity patterns and spatial use (Keuling et al., 2008; Maillard & Fournier, 2014; Miguel et al., 2020). Nevertheless, the effects caused by hunting on wild boar social organisation are uneven across sites and different studies do not agree on how wild boar respond to hunting (Massei et al., 2011; Podgórski & Śmietanka, 2018).

Group composition was only affected by population control driven hunts inside the reserves in one case, for Riudeteix in 2014/2015, when the proportion of matriarchal groups decreased whilst that of solitary males and subadults increased. This tendency was observed in all the other study cases, although the difference was not significant. These variations could be partly explained by regular season variations in group compositions. However, previous studies showed that the proportion of matriarchal groups during autumn and winter remain stable (Rosell et al., 2004), while the results of the present study show that there was a significant decrease during these periods in both study sites, supporting the idea that the hunting intervention was the cause of the severe reduction of the number of matriarchal groups observed. The fact that matriarchal groups decrease after disturbance can be attributed to these groups being more easily hunted as they are more detectable by hunting dogs, but also to the leading sows being more cautious and having a lower threshold of risk perception than subadults and solitary males, as suggested by (Saïd et al., 2012). Lacolina et al. (2009) reported that high hunting pressure may lead to an increase of aggregations of unrelated adult females suggesting that hunting may increase contact rates between otherwise different matriarchal groups. Wild boar group disruption, especially if the leading sow and other adult females are culled can also cause an increase of the juvenile dispersion (Moennig et al., 1999), once again leading to a potential increase in contact rate, which represents a major risk of disease transmission (Podgórski et al., 2018).

Little attention has been paid so far to the effect of hunting on wild boar social disruption, although the latter could have significant effects on disease control, particularly for those diseases that are contact-rate or density dependent. For instance, culling-induced social perturbation, reported in European badgers (*Meles meles*), led to increased contacts between neighbouring social groups

and was in turn associated to a rise of bovine tuberculosis prevalence (Riordan et al., 2011). Similar results were reported for alpine Ibex (*Capra Ibex*) as home range perturbations due to culling led to a brucellosis re-emergence (ANSES, 2015).

These findings have major implications for mitigating human-wild boar conflicts. In contexts where wild boar high densities are associated with negative impacts, such as crop damage, reduction of biodiversity, and vehicle collisions, reserves may act as sinks when hunting occurs in the surrounding grounds but also as sources of wild boar once the hunting season is over. This study suggests that single population control driven hunts carried out in non-hunted areas may achieve a significant reduction of individual numbers. Thus, banning hunting in some areas during a part of the hunting season will concentrate wild boar which will later allow to increase the effectiveness of methods such as culling or trapping.

These results are also relevant to manage disease outbreaks. For instance, current recommendations to control ASF include establishing a core area around the outbreak, surrounded by a buffer zone, which is in turn surrounded by an outer zone. Soon after the outbreak declaration, hunting is banned in the core and buffer zones and allowed only in the outer zone. After a certain time, the core and buffer areas are to be depopulated through intensive culling (Jori et al., 2020). Recent studies based on modelling of wild boar contact rates in North America, suggest that a 2 km culling radius around the disease detection might be sufficient to stop the spread, nevertheless, it would vary depending on the density and home range of the infected populations (Yang et al., 2021). The method used for culling should be chosen as the most efficient, causing the least possible disturbance and taking into account the local habitat and hunting traditions (Jori et al., 2020). In the study area driven hunt is by far the most used hunting method while other methods such as lying-in wait or stalking are barely practiced. The findings of this study confirm that regular driven hunts are an effective method of concentrating wild boar in relatively small areas where animals can then be removed by culling. Nevertheless, as highlighted by a recent study in South Korea, the human intervention in ASF infected areas represents an important risk of disease spread, particularly if biosecurity measures are not properly adopted, and trapping methods can be the most effective intervention in some situations (Jo & Gortázar, 2021).

The results of several studies suggest that driven hunts can increase the wild boar movements over wider areas (Maillard et al., 1996b; Sodeikat & Pohlmeier, 2003b) and cause group disruptions, as we found in the present study, potentially leading to an intensification of contacts with other wild boar groups and to an increased risk of disease transmission. Yang et al. (2021) did not detect any effect of culling on contact rates in low removal situations but suggest that higher culling pressure could lead to an increase of contact rate and disease spread.

The ‘reserve effect’ and the fact that wild boar densities temporary increase in non-hunted areas could also be exploited to maximise the impact of vaccination campaigns based on baits containing drugs such as classical swine Fever vaccines. Future studies should explore this idea and assess whether a temporary, hunting-induced increase in concentration of wild boar can be used to increase bait uptake.

4.1 Conclusions

This study corroborated the ‘reserve effect’ as wild boar use non-hunted areas as a refuge when hunting occurs in the surroundings. The results also demonstrate that exceptional population control driven hunts undertaken inside these areas, are an effective method in reducing number of individuals, but may also cause a disruption of wild boar social groups, potentially increasing contact rates between groups. These findings indicate that detecting or creating these refuge areas could be used to improve the efficiency of population control and to mitigate the conflicts caused by this species. The results also support the creation of different types of areas around outbreaks of diseases such as ASF, where culling is either banned or encouraged according to the need to reduce disease transmission and minimise wild boar movements between areas.

5 Acknowledgements

This research was supported by the Montseny natural park and the ‘Pla de Doctorats industrials’ of the Catalan Government. We thank our colleagues from Minuartia and the Montseny natural park rangers who carried out the field work and the support of the ‘Evolutionary ecology, behaviour and biodiversity conservation’ research group.

We would like to specially thank our colleagues Daniel Guinart, from Montseny natural park, and Ferran Navàs from Minuartia who provided valuable contributions that greatly assisted the research.

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5. General discussion

5.1 Main contributions

As described in the introduction, wild boar is one of the most challenging species to manage due to its adaptability, high reproductive rates and success in human-modified landscapes. A key barrier to effective management is often the lack of comprehensive, evidence-based strategies that integrate long-term data on population dynamics, environmental responses and density dependence. This thesis addresses these challenges by analysing wild boar populations in Mediterranean regions, using long-term datasets to assess environmental, demographic and management influences. The findings enhance understanding of wild boar management and offer insights that are applicable to other ungulates facing similar challenges in population growth, habitat use and human-wildlife conflicts.

The main contributions of the three chapters of this thesis described above are summarized in four main topics (Figure 5.1), including the ecological drivers of population dynamics, the density dependence detected in population growth and the proportion of breeding females, reproduction patterns and their variability, and hunting strategies and ‘reserve effect’ implications.

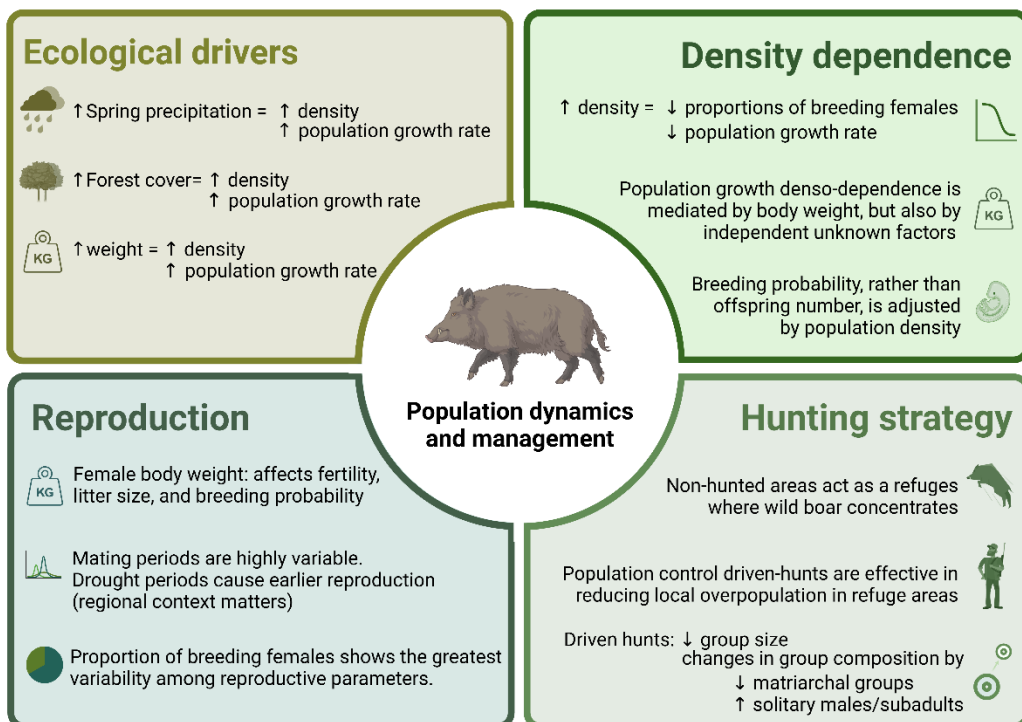


Figure 5.1. Synthesis of the main findings of the three chapters, organized in four main topics.

5.1.1 Ecological drivers of density and population growth

Wild boar populations in Mediterranean ecosystems are shaped by a complex interplay of factors. Regarding climate and landscape factors, spring precipitation emerged as a key driver of population trends, with increased rainfall positively affecting population density and growth in Mediterranean areas. This supports previous findings that drought can limit wild boar reproduction and survival (Bisi et al., 2018; Fernández-Llario & Carranza, 2000; Frauendorf et al., 2016; Uzal Fernandez & Nores, 2004). The long-term impact of reduced rainfall suggests that consecutive drought years may amplify population declines. Winter temperature also influences density but its effects on growth were less pronounced than in northern areas (Borowik et al., 2013). Higher forest covers, up to 80% of a local area, showed a strong positive association with both density and population growth, as they provide higher foraging and refuge opportunities for wild boar (Abaigar et al., 1994).

Female body weight also emerged as a key driver, with higher weights being linked to increased population densities and growth. This finding supports the widely known relationship between female body mass and higher reproductive output, and highlights the connection between resource availability, individual health and population dynamics (Aumaitre et al., 1982; Cellina, 2008; Frauendorf et al., 2016; Gamelon et al., 2017; Massei et al., 1996; Rosell, 1998; Sáez-Royuela & Telleria, 1987).

The current global change scenario also affects wild boar populations. As drought conditions are expected to become more frequent and severe, particularly in Mediterranean areas, reduced water and food availability may naturally limit wild boar population growth in many regions. However, the extent to which such climatic changes might aid in controlling population densities remains uncertain. Droughts could increase competition for resources, which may drive behavioural adaptations that allow populations to persist under harsher conditions. For example, using human resources such as irrigated crops, rubbish or domestic animals' food and water, among other factors, would potentially increase human-wild boar conflicts. In this case, restricting access to these anthropogenic resources would contribute to population control and conflict mitigation.

5.1.2 Density dependence in reproduction and population growth

Density-dependent processes were detected in this thesis, as the results showed that population growth decreases at higher densities. This aligns with findings in other ungulate species, such as moose, chamois, deer or bighorn (Brown, 2011;

Capurro et al., 1997; Coulson et al., 2000; Festa-Bianchet et al., 1998) and for wild boar (Imperio et al., 2012; Kapota & Saltz, 2018). However, other studies found no or a weak association between density and population growth, and suggested that density dependence is unlikely to limit wild boar population growth (Choquenot, 1998; Frauendorf et al., 2016; Ruf et al., 2021; Vetter et al., 2015).

The analysis also demonstrated a reproductive response of wild boar to density, driven by variation in breeding probability. At higher densities, fewer females breed, which highlights a mechanism similar to that observed in other ungulates (Albon et al., 1983; Coulson et al., 2000; Stewart et al., 2005) but not reported before in wild boar. This effect is partly mediated by female body weight, with heavier females being more likely to reproduce. This supports the hypothesis that increased competition for limited resources at higher densities compromises body condition and ultimately reduces reproductive success (Barasona et al., 2020; Frauendorf et al., 2016). Interestingly, a second mechanism, which is not mediated by body weight, is likely to contribute to the observed density-dependent effects on reproduction. Social dynamics, stress levels and competition for resources, among other factors, may influence breeding probability independently of body condition. For instance, changes in social structure or increased competition could affect mating opportunities or hormonal regulation and reduce the likelihood of pregnancy. These findings highlight the complex nature of density-dependent reproduction and the need for further research to understand these mechanisms.

Moreover, despite density-dependent regulations, wild boar populations continue to expand, which suggests that this process is not strong enough to stop population growth. This may be explained by the wide range of resources that wild boar can use –not only from natural habitats, but also from croplands and urban areas – as shown by previous studies that highlight the species' adaptability to diverse environments and food sources (Keuling et al., 2013; Massei et al., 2015). It is also relevant that short-term analyses failed to detect the density effects on female body weight, while they were captured in the long-term data set, which shows the need for extended monitoring to fully understand ecological processes.

5.1.3 Reproductive patterns variability

Breeding probability was the most flexible reproductive parameter compared to number of corpora lutea, litter size or intrauterine mortality. This suggests that wild boar respond to ecological changes (including population density) by varying the proportion of sows that reproduce rather than adjusting the number of offspring.

The lack of significant density effects on litter size and intrauterine mortality supports the notion that these parameters are relatively stable and less responsive to density variations in Mediterranean wild boar populations. As expected, female body weight consistently emerged as a critical determinant of reproductive success, influencing breeding probability and litter size (Aumaitre et al., 1982; Cellina, 2008; Frauendorf et al., 2016; Lombardini et al., 2014; Mauget, 1972; Rosell et al., 2012).

The study provides comprehensive data on key reproductive parameters, including litter size, fertility rates and intrauterine mortality. In general, these are consistent with findings in other Mediterranean wild boar populations but lower than values reported for northern regions (Abaigar, 1992; Brogi et al., 2022; Ditchkoff et al., 2012).

The observed earlier onset and prolonged duration of the mating period after dry years suggest that resource limitations may influence reproductive timing. These findings align with studies in other Mediterranean areas, which indicate that drought conditions can lead to earlier conception and less synchronous breeding (Brogi et al., 2022; Fernández-Llario & Mateos-Quesada, 2005). However, contrasting evidence from northern regions highlights the complexity and regional differences in these dynamics, with resource scarcity often delaying reproduction (Aumaitre et al., 1984; Cachelou et al., 2022).

5.1.4 Reserve effect and driven hunts effectiveness

This study confirms the reserve effect, where wild boar congregate in non-hunted areas when hunting occurs in the surrounding area, similarly to what has been described in previous studies both for wild boar and other ungulates (Frank et al., 2015; Grignolio et al., 2011; Sodeikat & Pohlmeier, 2003; Tolon & Baubet, 2010). Nevertheless, in other species such as moose, hunting disturbances were not found to have any effect on population movement (Neumann et al., 2009).

These temporary density increases can intensify local ecological impacts but they also present management opportunities. Population-driven hunts within reserves effectively reduce the number of individuals, with lasting effects observed up to 45 days post-hunt, which demonstrates the effectiveness of targeted interventions in these areas. Changes in group composition after driven hunts – such as an increase in solitary males and juveniles – may have implications for population dynamics and disease transmission. Hunting strategies should consider these social disruptions, as they could influence contact rates and the spread of density-dependent pathogens.

While reserves can unintentionally promote higher densities, they also offer a controlled setting for targeted interventions such as culling or disease management. The challenge lies in balancing conservation goals with effective population control strategies.

5.2 Recommendations for wild boar and other Mediterranean ungulates management

The management of human-wildlife conflicts aims to develop methods to achieve coexistence between humans and wildlife, while mitigating the reciprocal impacts (Náhlik et al., 2017). However, these efforts often overlook the complexities of wildlife dynamics, as traditional management strategies have primarily focused on controlling population growth through increased culling, often without considering variations in productivity or adapting the strategy based on factors such as when, where and how much culling is needed.

The findings of this thesis have significant implications and recommendations for wild boar management, and for other ungulate species (Figure 5.2). However, it is important to consider that wild boar has unique characteristics, including the highest reproductive rate among ungulates, an omnivorous diet, and an exceptional ability to adapt and habituate to human environments. These traits may limit the direct applicability of some findings to other species.

Each of the main topics explored – ecological drivers, density-dependent processes in reproduction and the reserve effect – provide valuable insights into how populations can be more effectively managed to achieve sustainable population densities and associated negative impacts on ecosystems and human activities.

5.2.1 *Predicting population dynamics to inform adaptive management*

Accurate predictions of density variation are essential for anticipating and planning management strategies, such as adjusting hunting efforts, implementing complementary culling techniques and non-lethal control measures in conflict areas, or identifying priority zones for habitat management. The findings on the main drivers of wild boar populations in Mediterranean areas will contribute to the elaboration of more accurate population predictions based on the interaction of different ecological variables for local populations in global change scenarios. Specifically, strategies should incorporate climate conditions so that hunting

strategies can be adjusted to increase pressure during years with favourable conditions, when survival rates and reproductive success are likely to be higher. This could further enhance the effectiveness of population control measures. However, it is also important to consider the potential cumulative effects of environmental conditions and hunting pressure. Although this is not a common situation, in cases of very low densities, if certain environmental factors – such as extreme droughts or particularly harsh winters – already lead to natural population declines, additional reductions due to hunting could overamplify the decline, potentially driving populations to critically low levels. While this scenario is not currently expected in any native distribution area, it should still be acknowledged in management planning to avoid unintended over-reduction of the population.

Another key finding of this thesis is the identification of density-dependent processes. Although the actual impact of these processes on the observed densities is not fully understood, it should also be considered for improving future population models.

In summary, the results highlight the need for predicting population dynamics to inform adaptative management, specifically:

- Strategies for population control and management must be based not only on current number of individuals but should also include robust modelling of future population trends, based on ecological drivers and reproductive patterns. This will allow for proactive adjustments in population control strategies by anticipating population changes.
- Long-term population and key drivers monitoring is key to adjust the predictions to regional conditions.
- Increasing the scientific knowledge of ecological responses to environmental drivers and the actual impact of density-dependence is key to improve evidence-based management.

5.2.2 Using 'reserve effect' areas for improving population control effectiveness

The detection of a 'reserve effect' presents both challenges and opportunities for management. Although it has been traditionally seen as a problem, causing an increase on local wild boar densities, these areas can be used as a tool to enhance control efforts. Key recommendations based on the findings include:

- 'Reserve effect' areas should be identified and used to enhance population control effectiveness. In them, highly efficient interventions can be conducted such as occasional drive hunts or trapping to reduce

local densities without negatively impacting broader ecosystems or non-target species.

- Reserve areas can be designated within hunting grounds where captures are used as part of targeted interventions. These areas, acting as refuges, concentrate high population densities, which allows the application of highly effective techniques to reduce local populations.
- Non-hunting reserves can be incorporated into disease management strategies, such as vaccination campaigns, by directing ungulates into these areas for easier monitoring and control.

5.2.3 Adapting habitats to reduce wildlife refuges near sensitive areas

As the results suggest that areas with dense forest covers are associated with higher wild boar density, reducing dense vegetation areas near urban environments and other conflict areas could further contribute to conflict mitigation. Moreover, previous studies have shown that wild boar use natural corridors, such as streams, especially those with dense vegetation to enter urban areas (Castillo-Contreras et al., 2018). Therefore, it is recommended that habitat management measures include:

- Clear dense vegetation areas close to sensitive and conflictive locations, such as urban areas or agricultural lands will contribute to avoiding individuals' concentration in these areas, which will reduce human-wildlife conflicts.
- Alternatively, target dense vegetation areas close to conflictive locations to optimise the trapping of relatively large number of individuals that use these areas as "urban refuges".
- Eliminate attractive habitats for ungulates on the verges of linear infrastructures, such as railway and roads, to contribute to reducing the risk of traffic accidents.

5.2.4 Reducing anthropogenic food availability

Due to the high adaptability of wild boar, its reliance on human-related food (such as crops, urban waste or domestic animals' food) is likely to increase during drought years. As anthropogenic food provides highly nutritious resources that improve female fitness (Castillo-Contreras et al., 2021) and the reproductive output of the populations (Rosell et al., 2012), which are not dependent on weather conditions, it is also expected that the likelihood of wild boar-human conflicts will increase during dry years. Other Mediterranean ungulates, such as roe deer, red deer or fallow deer, have a more limited ability to shift to anthropogenic food sources, as they are less

opportunistic and rely heavily on natural vegetation. However, they also increasingly use irrigated crops, orchards and suburban gardens, which leads to localized conflicts with humans (Ferretti et al., 2011; Heurich et al., 2015; Schwegmann et al., 2023). To effectively address conflicts and control population growth, it is essential to implement management strategies aimed at reducing the availability of anthropogenic food sources. The findings of this thesis show that food availability, represented by female body weight, influences density and reproduction variation. Therefore, strategies should include:

- Restricting access to all types of anthropogenic food sources, including limiting access to crop fields through fencing or other exclusion methods, securing garbage bins and avoiding access to human waste and restricting access to domestic animals' food, among others.
- Avoid providing any type of supplementary feeding, both in the urban and rural environment. This is key to achieve human-wildlife coexistence and sustainable population densities. Educating stakeholders about the ecological impacts of supplementary feeding and enforcing regulations to restrict this practice is key to achieve this.
- Such measures can help to reduce the attraction to urban areas and human habituation of individuals, but also to avoid increasing reproductive rates, which are strongly linked to females' fitness conditions.

All the recommendations and strategies require collaboration among hunters, wildlife managers, and public authorities to ensure their successful implementation, as well as recurrent monitoring of their effectiveness and adaptation to changing circumstances.

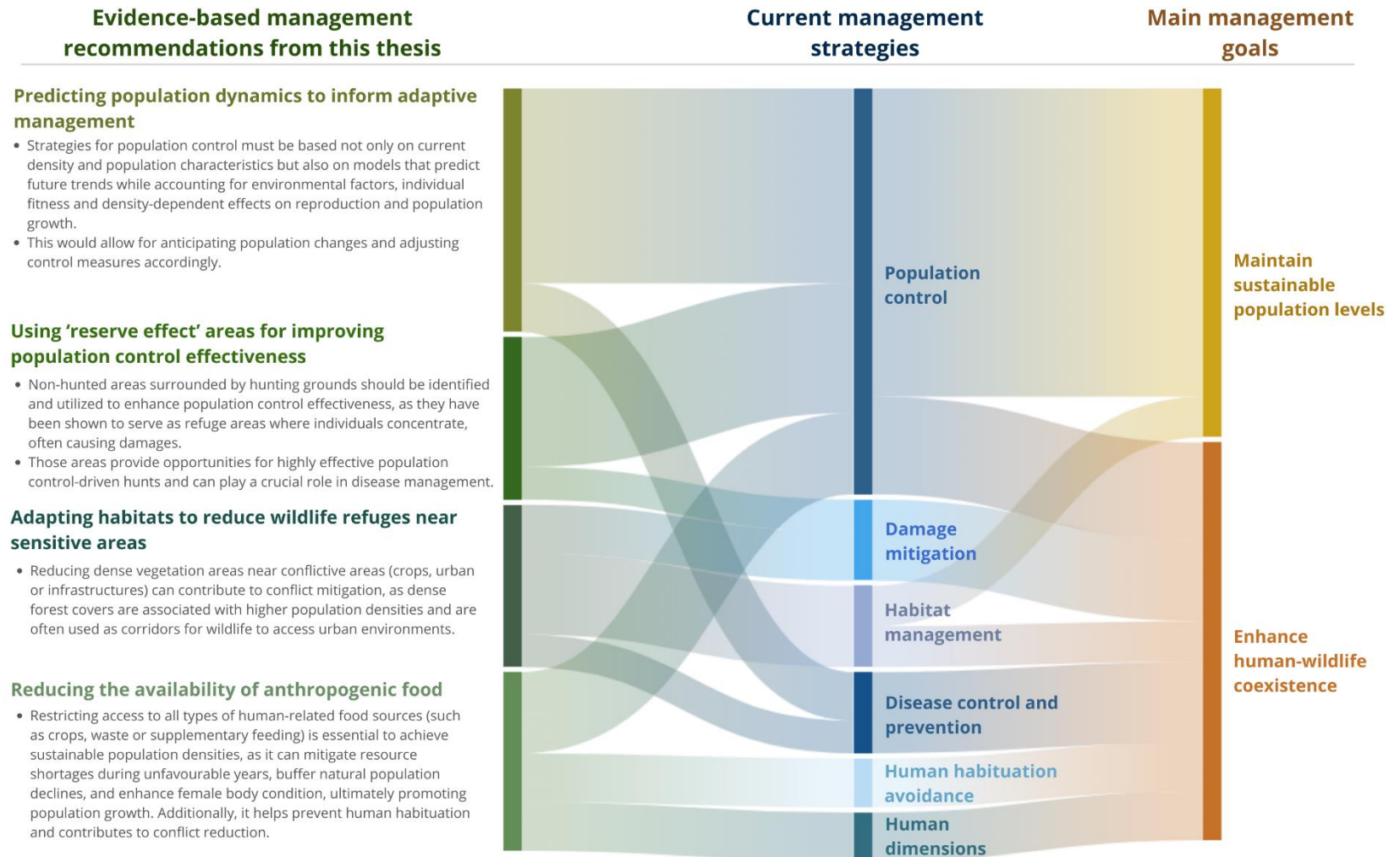


Figure 5.2. Management recommendations from this thesis and contributions to current management strategies and goals.

5.3 Further research

The findings revealed knowledge gaps and highlighted several key areas for future research and management. First, long-term monitoring programmes should be expanded to incorporate additional environmental variables, such as climate, vegetation dynamics and seasonal fluctuations in food availability, particularly forest fruits like acorns and other key resources such as crops. Standardizing the collection of data on resource availability will allow for a more comprehensive understanding of how changes in resource abundance influence wild boar populations. Integrating these data into predictive models could help to forecast population trends more accurately and inform more effective management strategies.

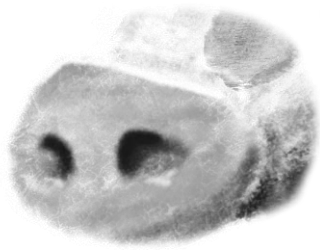
Since the number of wild boar hunted could not be incorporated into the models as a mortality indicator, it was not possible to evaluate its direct impact on population dynamics. This was due to the fact that hunting data were used for density calculations and, therefore, could not be included as an explanatory variable in the models. Exploring the effect of the number of individuals hunted on population dynamics would provide valuable insights into the impact of hunting on wild boar populations.

The long-term effects of climate change on wild boar populations remain largely uncertain. As precipitation patterns and temperatures continue to shift, the availability of vital resources, such as food and water, may change, potentially altering population dynamics in complex ways. Further research is needed to understand how climate change may influence wild boar behaviour, distribution, and reproduction, and how management strategies can be adapted to address these challenges in the future.

Regarding density dependence in reproduction and population growth, the mechanisms through which it operates are still not fully understood, and questions remain open. It would be interesting to evaluate the effects of density on parameters such as social structure, individual stress, behaviour, or hormonal variations, among others, and better understand how these might affect reproduction parameters and thus population growth. Moreover, the interaction of density-dependent processes with environmental factors, as well as across different ecological and climatic contexts, remains unclear and requires further investigation. Comparative studies across sites and regions, could provide valuable insights into how these interactions function under different

conditions. Such studies could help clarify the underlying mechanisms and improve our understanding of the role of density dependence in population dynamics in diverse environments.

In addition, experimental studies testing the effectiveness of various management interventions, such as habitat modification, reserve-based strategies, and control measures, should be pursued. These studies could provide valuable insights into which approaches provide the best outcomes in terms of reducing human-wild boar conflicts and ensuring sustainable population management. Understanding the effectiveness of strategies under varying ecological conditions would contribute significantly to improving population management practices.



6. Conclusions

1. **Spring precipitation (both current and previous year), female weight, and forest cover are strong drivers of wild boar densities and population growth rates.** The interaction between crop cover and total annual precipitation also plays a significant role in shaping population density. While winter temperature influenced density, it had no effect on growth rate in the study area. The limiting effect of spring precipitation on wild boar density identified in this study is expected to become more critical in the coming decades, as precipitation is projected to decrease in Mediterranean regions. Given the high adaptability of wild boar, their dependence on human-supplied food is likely to increase, worsening the risk of wild boar-human conflicts as droughts become more frequent.
2. **Density-dependence is observed in wild boar population growth rate and reproduction.** Higher densities are associated with a lower proportion of females breeding and lower population growth in the subsequent years. This relationship is partly mediated by female body weight, but also by other mechanism, independent of body weight. This suggests that other unknown factors - such as social structure, behaviour, stress, or disease - may play a role.
3. **Primary reproductive adjustment to varying wild boar population density lies in whether a female becomes pregnant, rather than in the number of offspring produced.** No other parameter, apart from breeding probability, was found to be directly influenced by population density variations. The proportion of pregnant females is also the breeding parameter that shows the greatest variation, influenced by changes in environmental parameters.
4. **Female body weight was a consistent and significant positive predictor of reproductive success.** Heavier females exhibited higher fertility, larger litter sizes, and greater breeding probabilities. These findings reinforce previous research and show the importance of body condition in determining reproductive output in wild boar.
5. **Mating period showed notable variation,** with the 2023 mating period being earlier and longer compared to previous years, likely due to reduced resource availability following drought conditions in 2022. While this aligns with some studies showing earlier conceptions in dry conditions, it contrasts with other research suggesting that low resource availability generally delays reproduction. This indicates that the effect of resource limitation on reproductive timing depends on regional ecological contexts.
6. **The proportion of breeding females showed high variability among years and study areas, ranging from 29% to 81%,** this variability is the main cause of the significant population fluctuations observed between locations and years. This variability supports previous findings that breeding success is one of the most flexible reproductive parameters in these populations.

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7. **A 'reserve effect' was detected in the study area**, where wild boar temporarily concentrate in non-hunted areas during the hunting season in response to surrounding hunting pressure. This behavioural shift may lead to localized and temporary overpopulation in these areas.
 8. **Occasional population control-driven hunts in these areas are effective at reducing the number of individuals** for up to 45 days. This reduction is both due to the animals culled and animals that abandon the refuge areas, and thus, may be culled in the surrounding hunting grounds.
 9. **Driven hunts lead to group size reductions and group composition changes**. After the driven hunts the proportion of matriarchal groups decreased while solitary males and subadults increased. This shift may be due to matriarchal groups being more easily hunted as they are more detectable. It could also be due to the leading sows' heightened caution and lower risk tolerance, causing them to take longer to return to the hunted area where the driven hunt was conducted.
 10. **Long-term datasets are essential for detecting density-dependent effects**, as the broader 23-year dataset revealed a significant negative relationship between density and female body weight, which was not detectable in the shorter, three-year dataset. This highlights the need for extended monitoring to capture the full extent of ecological processes.
 11. **Adaptive management strategies, guided by accurate population dynamics predictions, are crucial for promoting human-wild boar coexistence and achieving sustainable population levels**. As climate change is expected to strongly affect wild boar populations—both by reducing the availability of food from natural areas and by influencing reproductive parameters—there is an urgent need for flexible and responsive management approaches. These should integrate climate and ecological data, enabling proactive responses to the evolving dynamics of wild boar populations and their interactions with humans.



7. General references

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8. Appendix

Chapter 1 Supplementary materials

Table S1. Description of the calculation method and source of each explanatory variable included in the models.

Variable	Description	Source
CY winter precipitation	Sum of precipitation in January, February and March of the current year in each site	SMC ¹
CY Spring precipitation	Sum of precipitation in April, May and June of the current year in each site	SMC
CY Summer precipitation	Sum of precipitation in July, August and September of the current year in each site	SMC
PY winter precipitation	Sum of precipitation in January, February and March of the previous year in each site	SMC
PY Spring precipitation	Sum of precipitation in April, May and June of the previous year in each site	SMC
PY Summer precipitation	Sum of precipitation in July, August and September of the previous year in each site	SMC
PY Autumn precipitation	Sum of precipitation in October, November and December of the previous year in each site	SMC
CY total precipitation	Sum of the total yearly precipitation in each site	SMC
PY Winter temperature	Mean daily temperature during January, February and March	SMC
PY Spring temperature	Mean daily temperature during April, May and June of the previous year for each site	SMC
PY Summer temperature	Mean daily temperature during July, August and September of the previous year for each site	SMC
PY Autumn temperature	Mean daily temperature during October, November and December of the previous year for each site	SMC
Percentage of crop surface	Percentage of any type of crop cover among the total site surface	ICGC ²
Percentage of forest surface	Percentage of any type of forest cover among the total site surface	ICGC
Previous year female weigh	Mean weigh of females hunted	CWBMP ³

¹ Catalan Meteorological Service

² Cartography and Geology Institute of Catalonia

³ Catalan Wild boar monitoring program

Table S2. Summary of the female weight mean, standard deviation (SD) and sample size (N) for each site and hunting season.

Site	Female weight	1998/1999	1999/2000	2000/2001	2001/2002	2002/2003	2003/2004	2004/2005	2005/2006	2006/2007	2007/2008	2008/2009	2009/2010	2010/2011	2011/2012	2012/2013	2013/2014	2014/2015	2015/2016	2016/2017	2017/2018	2018/2019	2019/2020	2020/2021	2021/2022
1. Alt empordà	Mean	41,7	43,6	40,4	41,6	44,9	41,2	42,4	43,9	41,5	41,2	41,9	40,2	43,7	41,6	39,9	40,5	42,8	42,1	38,5	40,2	41,2	38,7	45,7	42,0
	SD	16,4	16,4	16,2	16,4	17,5	16,3	15,9	17,3	15,7	15,6	16,4	16,5	17,4	17,4	15,5	16,5	17,5	17,3	16,0	16,4	16,9	17,6	17,6	18,0
	N	331	188	221	276	249	292	315	327	236	244	236	354	257	246	323	332	317	406	412	451	414	585	305	480
2. Z.V.Garrotxa	Mean	41,4	43,0	40,4	40,2	40,1	42,8	41,1	44,1	41,5	46,0	42,5	44,3	44,0	42,2	40,5	42,5	43,2	42,6	39,8	41,1	40,5	38,4	39,8	39,0
	SD	15,1	15,9	15,0	16,4	14,5	17,3	16,8	16,6	17,1	18,7	15,6	16,4	17,3	16,2	16,2	17,0	16,8	16,4	16,8	16,9	16,0	16,2	15,8	16,5
	N	276	181	222	282	234	312	236	297	368	494	322	533	601	999	1167	1037	1117	1214	1155	1113	660	911	895	1514
3. Gavarres	Mean	-	-	-	-	-	-	-	42,3	44,9	44,1	44,7	44,9	47,4	45,0	44,2	41,7	44,8	42,6	42,0	43,2	45,2	44,0	43,4	43,4
	SD	-	-	-	-	-	-	-	15,6	17,0	17,8	17,2	16,2	18,3	19,5	17,7	18,7	17,5	16,8	17,9	17,9	17,1	17,0	18,6	17,9
	N	-	-	-	-	-	-	-	162	538	635	436	596	420	676	628	897	862	1092	1156	870	972	1259	1226	2115
4. Montseny	Mean	-	-	39,3	40,5	45,2	40,1	42,4	43,5	42,0	41,4	42,2	41,7	43,5	41,8	43,2	44,5	45,2	41,7	42,1	40,2	42,1	41,1	43,0	39,9
	SD	-	-	13,3	14,6	14,5	15,2	14,6	15,8	15,3	15,7	14,7	15,9	15,6	15,5	15,7	16,8	15,4	15,2	15,8	15,0	16,3	17,6	17,3	17,1
	N	-	-	312	405	385	604	508	644	567	693	524	699	578	768	949	1076	1088	1537	1339	1033	1030	1340	1087	1530
5. Montnegre-Corredor	Mean	-	-	-	48,5	51,6	49,4	48,0	49,9	48,4	47,5	51,9	48,2	50,0	48,7	48,4	49,7	49,1	48,2	48,1	44,4	46,2	45,8	46,9	46,1
	SD	-	-	-	16,6	15,6	17,3	18,7	17,4	16,8	17,6	17,4	17,7	17,9	16,8	16,7	17,2	16,6	18,1	17,0	16,7	17,5	17,6	17,2	18,5
	N	-	-	-	113	89	254	136	228	238	348	233	372	226	370	516	489	488	647	642	530	580	673	656	676
6. Serr. Litoral i Marina	Mean	-	-	-	-	-	-	-	51,7	49,8	40,0	48,2	48,4	47,6	45,4	51,4	51,3	50,1	38,2	51,9	47,2	42,7	47,9	42,0	45,2
	SD	-	-	-	-	-	-	-	15,4	13,2	13,4	16,5	17,4	15,5	16,6	17,4	17,0	18,5	16,2	17,1	19,2	19,3	19,8	17,4	18,2
	N	-	-	-	-	-	-	-	21	124	86	78	57	60	104	97	162	118	109	142	165	158	143	156	169
7. Sant Llorenç del Munt	Mean	45,4	49,0	48,9	42,6	48,5	45,0	45,8	44,2	47,4	52,8	46,0	45,9	48,5	45,2	47,0	44,5	47,6	46,9	42,7	47,8	47,0	42,6	46,5	44,1
	SD	15,3	17,3	17,1	15,4	17,0	16,5	16,2	17,8	15,7	17,8	17,4	17,0	14,8	15,6	16,1	18,0	17,7	17,8	18,6	17,2	17,4	19,0	19,2	18,7
	N	67	63	45	117	69	84	113	140	144	149	111	195	118	130	156	281	256	329	349	332	369	279	378	393
8. Garraf-olèrdola-Foix	Mean	-	-	45,4	58,3	49,7	60,9	54,8	44,5	43,7	52,7	51,0	46,6	48,3	51,4	48,8	49,2	51,0	48,5	40,4	45,8	49,0	48,4	47,2	44,6
	SD	-	-	15,5	14,4	16,7	16,6	15,1	15,3	12,6	10,8	16,4	17,7	16,0	16,2	18,2	14,7	17,1	12,1	16,8	14,9	16,0	16,0	16,7	15,8
	N	-	-	22	15	20	12	23	14	31	27	65	59	36	70	157	139	192	173	221	190	206	261	304	305
9. Freser-Setcases	Mean	45,1	53,0	49,3	45,4	47,7	46,0	45,1	46,5	42,7	44,2	44,6	43,3	43,5	43,9	43,6	42,3	46,3	43,1	44,1	41,2	43,6	40,1	44,4	42,5
	SD	13,5	14,5	16,4	14,8	14,3	19,0	14,9	16,2	16,8	16,4	15,3	16,5	15,6	17,5	18,1	17,9	17,6	16,4	17,2	15,7	17,5	16,6	17,2	17,1
	N	150	85	113	126	82	142	136	177	142	218	198	163	167	87	203	206	254	339	392	339	230	312	197	346
10. Cadí	Mean	31,0	46,9	41,3	44,5	48,5	46,5	45,0	43,6	52,0	43,3	46,5	46,6	45,9	42,0	46,0	45,7	49,8	52,4	46,7	46,8	49,7	47,0	49,5	45,5
	SD	12,4	16,5	16,6	16,4	16,5	16,0	16,3	17,4	18,5	17,9	16,2	14,8	18,1	18,3	17,8	19,8	16,3	17,5	17,8	14,6	19,6	17,1	18,5	16,4
	N	13	109	162	228	153	208	243	128	63	197	131	99	82	67	80	89	83	124	234	172	119	104	150	134

Table S2 (cont.). Summary of the female weight mean, standard deviation (SD) and sample size (N) for each site and hunting season.

Site	Female weight	1998/1999	1999/2000	2000/2001	2001/2002	2002/2003	2003/2004	2004/2005	2005/2006	2006/2007	2007/2008	2008/2009	2009/2010	2010/2011	2011/2012	2012/2013	2013/2014	2014/2015	2015/2016	2016/2017	2017/2018	2018/2019	2019/2020	2020/2021	2021/2022
11. Boumort	Mean	39,3	43,4	39,4	43,4	49,1	41,7	35,7	55,0	49,4	NA	45,7	39,4	47,1	43,9	45,6	45,4	50,8	42,4	40,9	37,6	43,1	44,1	46,1	45,2
	SD	14,5	10,3	15,1	15,1	11,9	10,4	14,8	8,7	10,2	NA	23,0	18,6	16,0	17,9	17,8	15,6	14,8	14,3	13,3	14,6	12,2	23,4	15,4	11,2
	N	64	46	140	80	32	25	73	36	16	NA	45	30	83	78	42	83	85	163	136	199	73	57	154	136
12. Muntanyes de Prades	Mean	-	-	-	-	-	51,3	49,3	47,8	46,0	46,1	46,9	47,7	45,8	45,4	46,2	44,5	46,5	43,8	45,7	41,3	44,5	43,0	44,8	46,4
	SD	-	-	-	-	-	14,9	15,1	16,4	13,9	15,9	14,6	15,7	16,9	15,7	17,5	15,1	14,2	14,9	16,3	12,9	13,2	12,9	15,1	15,0
	N	-	-	-	-	-	128	131	263	191	250	206	261	250	203	185	382	241	418	457	406	399	240	304	325
13. Montsant	Mean	-	-	-	-	-	56,1	50,4	52,3	49,3	49,1	50,5	50,7	46,1	46,9	43,6	42,1	45,3	45,5	43,4	44,6	48,2	48,6	43,3	43,6
	SD	-	-	-	-	-	13,7	14,1	17,1	15,0	16,8	18,0	17,1	15,1	12,1	15,9	15,6	15,7	15,2	16,0	15,3	16,9	13,7	15,8	14,8
	N	-	-	-	-	-	22	23	47	45	55	82	85	104	103	99	149	138	241	216	204	183	193	228	248
14. Ports de Tortosa i Beseit	Mean	36,2	33,6	33,9	34,6	37,0	36,6	39,0	40,3	37,7	36,1	36,2	37,0	40,4	38,6	46,3	42,1	45,9	45,4	42,5	39,5	42,1	44,7	42,9	45,0
	SD	15,4	14,2	16,6	16,7	16,1	15,1	15,8	16,1	15,4	16,0	17,0	15,2	14,2	16,0	16,5	17,8	15,7	14,9	16,7	15,0	16,5	16,6	16,7	17,1
	N	135	46	70	77	122	162	157	167	160	171	122	149	185	138	153	132	120	112	120	99	92	97	108	112

Models validation

The goodness-of-fit and diagnostic assessments for the generalized additive model (GAM) were conducted using the `gam.check` function from the `mgcv` package (version 1.8-40) in R (R Core Team, 2022). The `gam.check` function provides insights into the appropriateness of the fitted GAM and helps identify potential issues.

Figure S1 shows summary plots from the 'Density model', and Figure S2 from the 'Growth rate model'

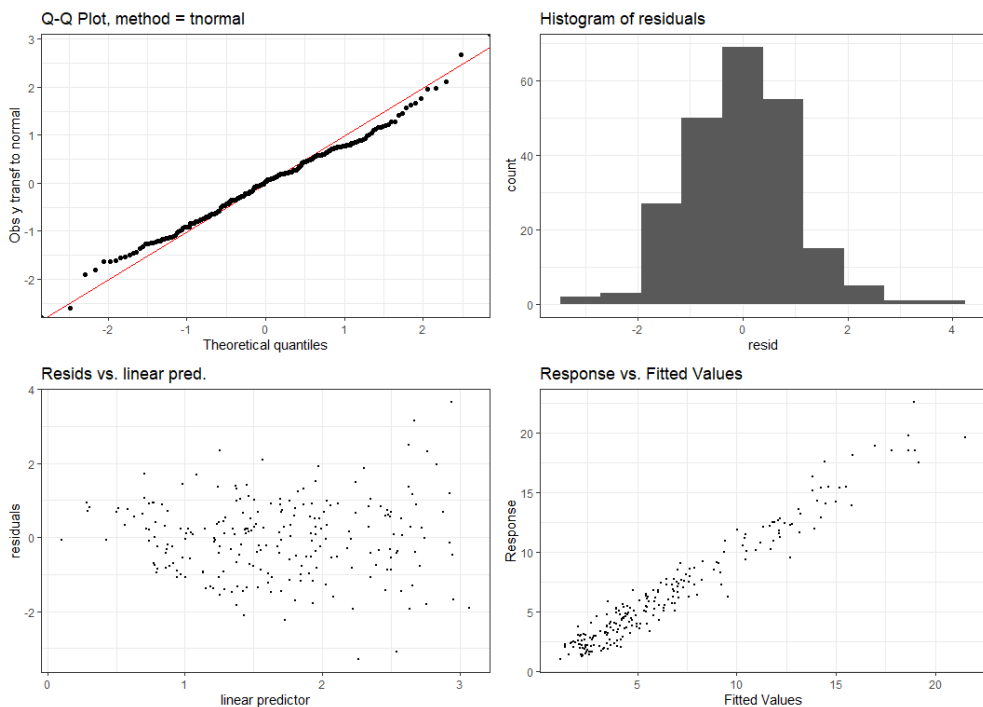


Figure S1. Basic residual plots (normal Q-Q, histogram of residuals, residuals against linear prediction and response against fitted values) for checking the generalized additive mixed model (GAMM) model fitting process for the 'Density model'.

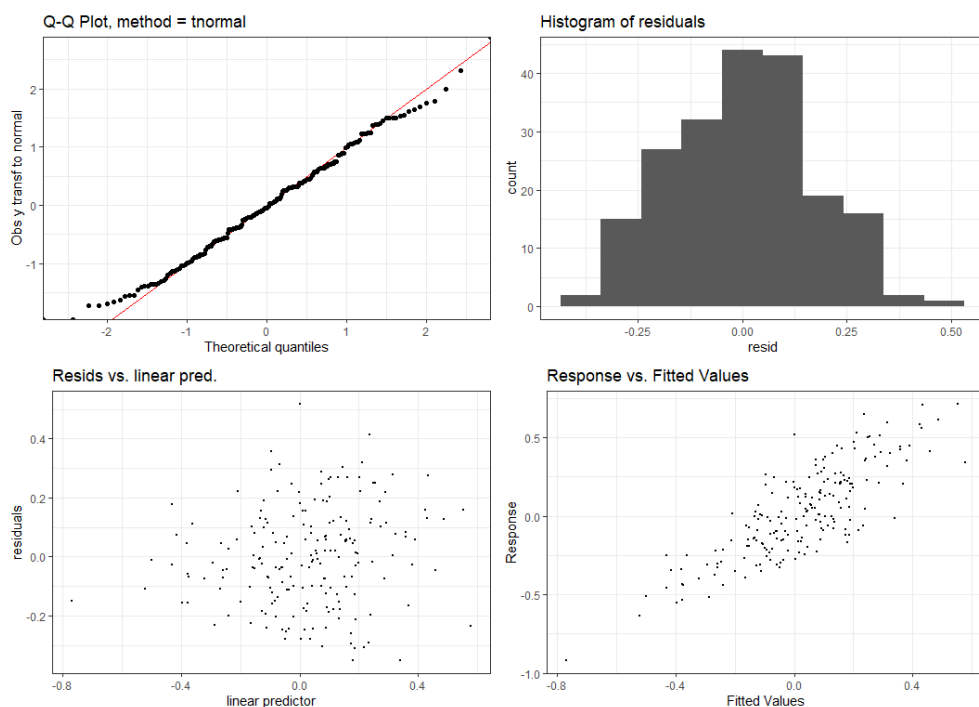


Figure S2. Basic residual plots (normal Q-Q, histogram of residuals, residuals against linear prediction and response against fitted values) for checking the generalized additive mixed model (GAMM) model fitting process for the ‘Growth rate’.

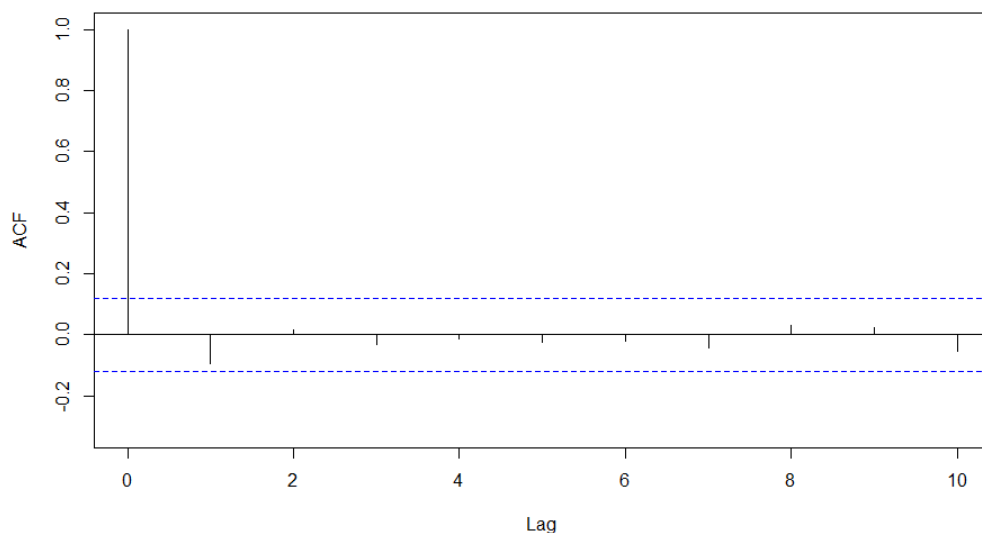


Figure S3. Autocorrelation Function (ACF) plot showing the correlation of the population growth data at different lags. The blue dashed lines indicate the point of statistical significance, with values outside these lines being considered significant. The correlation at lag 0 is always 1 by definition, as it represents the correlation of the series with itself.

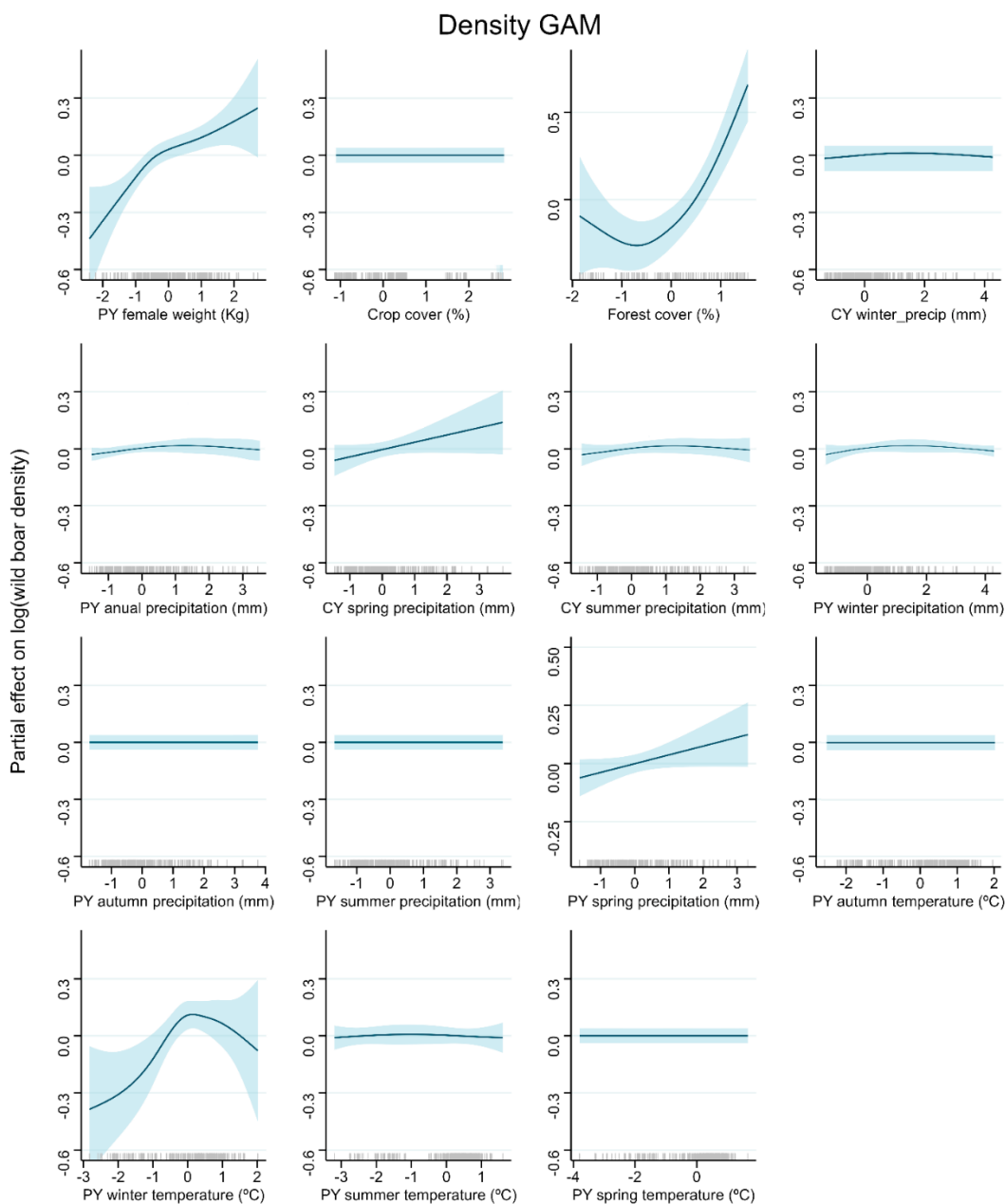


Figure S4. Effects of different factors on wild boar density in Catalonia derived from the results of generalized additive mixed models (GAMMs). The distribution of explanatory variable values is marked with grey vertical lines on the x-axis. The y-axis shows the predicted value of the response variable for a given predictor variable, while holding all other predictor variables at their average. Blue shadow represents the 95% confidence intervals.

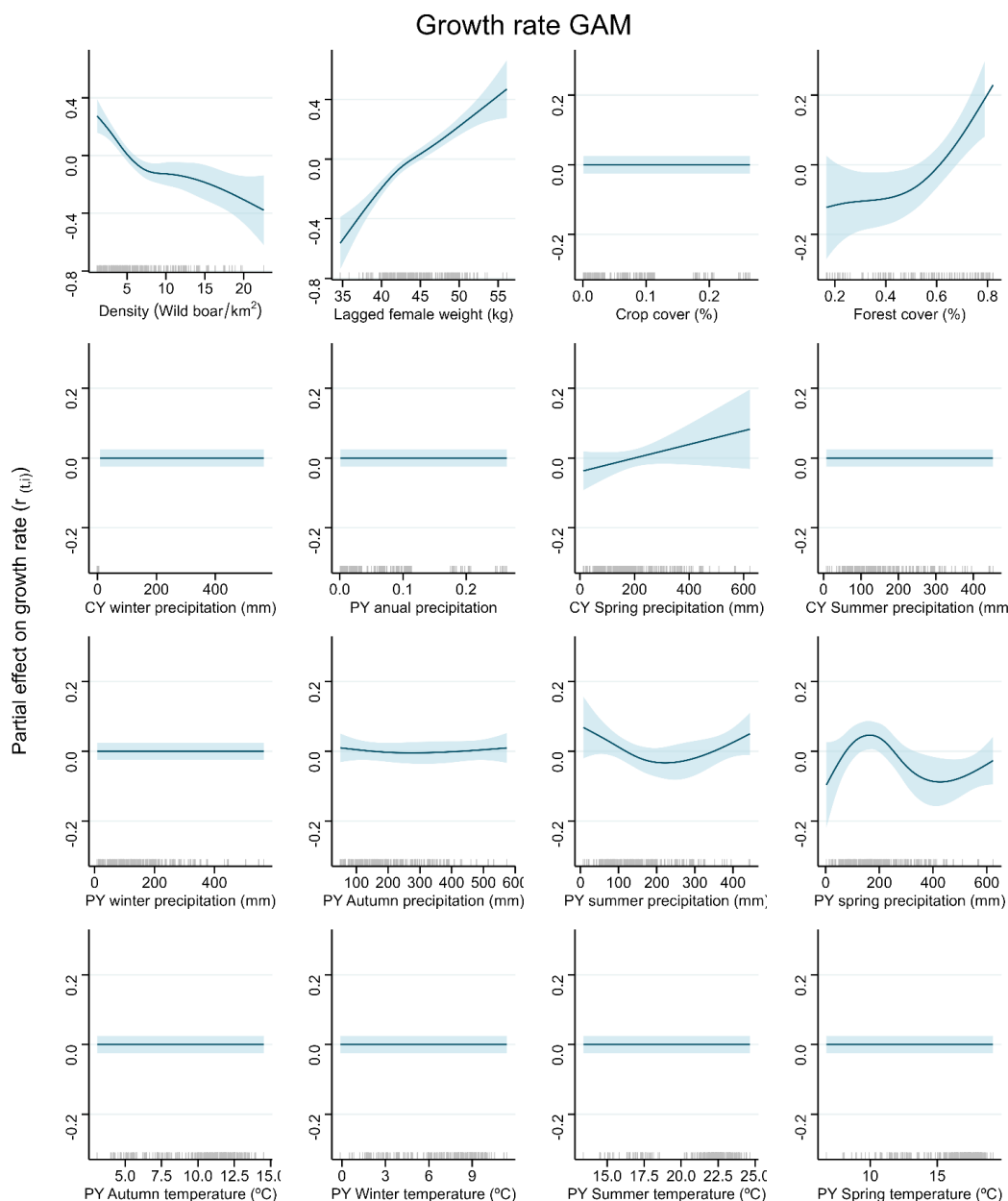


Figure S5. Effects of different factors on wild boar population growth rate in Catalonia derived from the results of generalized additive mixed models (GAMMs). The distribution of explanatory variable values is marked with grey vertical lines on the x-axis. The y-axis shows the predicted value of the response variable for a given predictor variable, while holding all other predictor variables at their average. Blue shadow represents the 95% confidence intervals.

Chapter 2 Supplementary materials

Table A1. Results of the *number of corpora lutea* model, including female weight (W), current year population density (D_t) and previous year density (D_{t-1}) as explanatory variables, and site as a random factor, the model included all observations with complete data ($n=264$). Significance codes: $^{**}p<0.05$.

Predictors	Estimate	SD	z value	Pr(> z) value	Effect
W - Female body weight	0.006	0.002	2.737	0.018 *	Increased corpora lutea with higher female body weight
D_t - Current population density	-0.016	0.007	-0.225	0.82	No effect of current year population density
D_{t-1} - Previous year density	0.002	0.007	0.311	0.76	No effect of previous year population density
Random effect	Variance	Std. Dev			
Site	0.0153	0.1239			
Response variable					
Number of corpora lutea					

Table A2. Results of the *litter size* model, including female weight (W), current year population density (D_t) and previous year density (D_{t-1}) as explanatory variables, and site as a random factor, the model included all observations with complete data ($n=288$). Significance codes: $^{***}p<0.01$.

Predictors	Estimate	SD	z value	Pr(> z) value	Effect
W - Female body weight	0.115	0.041	2.841	0.0045 **	Increased litter size with higher female body weight
D_t - Current population density	0.061	0.042	1.469	0.1418	No effect of current year population density
D_{t-1} - Previous year density	-0.077	0.044	-1.757	0.0790	No effect of previous year population density
Random effect	Variance	Std. Dev			
Site	3.433e-4	0.0185			
Response variable					
Litter size (Number of foetus)					

Table A3. Results of the *intrauterine mortality* model, including female weight (W), current year population density (D_t) and previous year density (D_{t-1}) as explanatory variables, and site as a random factor, the model included all observations with complete data ($n=171$).

Variable	Estimate	SD	Z value	Pr(> z) value	Effect
W - Female body weight	-0.011	0.007	-1.395	0.163	No effect of female body weight
D_t - Population density	-0.043	0.021	-2.011	0.347	No effect of current year population density
D_{t-1} - Previous year density	0.034	0.020	1.695	0.090	No effect of previous year population density
Random effect	Variance	Std. Dev			
Site	2.212e-09	4.704e-05			
Response variable					
Intrauterine mortality (proportion of reduction from N corporea lutea to N foetus)					

Table A4. Missing paths output and standardized path coefficients the best path model retained (see Table 3 for symbols).

	missing.path	Test.Type	DF	Crit.value	p.value
1	$M \sim D_{t-1}$	coef	40.1401	0.3841	0.5389
			Std_estimat		
	Response	predictor	e	p.value	
	M	D_t	0.0639	0.3315	
	BP	M	0.4393	<0.001	
	BP	D_t	-0.4116	<0.001	
	BP	D_{t-1}	-0.5942	<0.001	
	D_t	D_{t-1}	-0.4506	<0.001	

Chapter 3 Supplementary materials

S1. Wild boar group size mean, standard error and range for each site and study period, during the Non-hunting and hunting seasons in the Montseny Natural Park.

Variable	Riudeteix				Vallforneres			
	2014 – 2015		2015 – 2016		2014 – 2015		2015 - 2016	
	Non-hunting	Hunting	Non-hunting	Hunting	Non-hunting	Hunting	Non-hunting	Hunting
Group size	1.65	2.07	1.43	2.04	1.40	2.47	1.80	2.86
±SE	0.13	0.21	0.09	0.18	0.07	0.28	0.07	0.23
Min – Max	1-20	1-13	1-6	1-7	1-6	1-9	1-12	1-15

S2. Wild boar group size mean, standard error and range for each site and study period, before and after the population control hunt inside the reserves in the Montseny Natural Park. The 'after' period includes 45 days after the population control hunt.

Site	Variable	2012 – 2013		2013 – 2014		2014 – 2015		2015 - 2016	
		Before	After	Before	After	Before	After	Before	After
Riudeteix	Group size	2.38	2.18	2.28	1.37	2.07	1.64	2.04	1.46
	±SE	0.14	0.22	1.66	0.23	0.21	0.12	0.18	0.08
	Min – Max	1-12	1-9	1-19	1-5	1-13	1-20	1-7	1-6
Vallforneres	Group size	-	-	1.89	1.06	2.47	1.54	2.86	1.84
	±SE	-	-	0.07	0.05	0.28	0.10	0.24	0.06
	Min – Max	-	-	1-11	1-2	1-9	1-15	1-15	1-12

9. Original publications



What drives wild boar density and population growth in Mediterranean environments?

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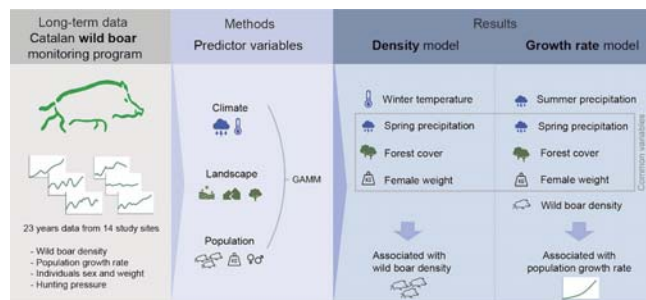
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HIGHLIGHTS

- Effective wildlife management requires accurate predictions of population fluctuations.
- Two models explored factors affecting wild boar density and population growth rate.
- Spring precipitation, forest cover and female weight positively affect wild boar density and population growth.
- Density dependent processes affect wild boar population dynamics.

GRAPHICAL ABSTRACT



ARTICLE INFO

Editor: Rafael Mateo

Keywords:

Population dynamics
Environmental factors
Density dependence
Wildlife management
Human-wildlife conflict
Sus scrofa

ABSTRACT

Accurate prediction of fluctuations of wildlife local number of individuals is crucial for effective population management to minimise human-wildlife conflicts. Climate, habitat, food availability, and density dependence are among the main factors influencing mammalian population dynamics. In southern Europe, precipitation and temperature, particularly during summer have been suggested as key factors affecting wild boar (*Sus scrofa* L.). However, there is uncertainty regarding the role of these factors and the mechanisms driving population fluctuations. This study utilized long-term data of wild boar populations from 14 study sites collected for 23 years in Catalonia, Spain, to analyse the factors that drive population density and growth rate. Generalized Additive Mixed Models (GAMM) explained respectively, 94 % and 65 % of the density and growth rate variability. Spring precipitation in both current and previous year, female weight, and forest cover (particularly above 60 %) were directly associated with higher wild boar densities and population growth rates. The interaction between crop cover and total annual precipitation also played a significant role in determining population density. Higher densities were linked to lower population growth in the following year, likely due to a density-dependent process. These results suggest that the expected decrease in rainfall linked with global warming may limit the

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availability of natural resources and potentially slow wild boar population growth. Nevertheless, wild boar can exploit alternative anthropogenic food sources, potentially leading to an increase of human-wildlife conflicts. Therefore, incorporating management policies aimed at restricting wild boar access to human food sources is key for controlling their reproductive output. Additionally, landscape management strategies targeted at diminishing refuge and resource availability in regions experiencing high wild boar impact are essential for contributing to sustainable coexistence between wild boars and human populations.

1. Introduction

Wildlife population dynamics is affected by birth, death, immigration, and emigration, which are in turn influenced by many factors including climate, habitat, food availability, population density and age structure (Krebs, 2002; Moss et al., 1982).

Understanding how these factors influence wild boar (*Sus scrofa* L.) population dynamics is crucial for reliable population forecast and effective management strategies. For instance, the EFSA Panel on Animal Health and Welfare (AHAW) (ENETWILD - consortium et al., 2022) highlighted the need for comprehensive collection and analysis of data on wild boar population dynamics to identify the key demographic drivers associated with this species and improve wild boar management.

The economic impacts of wild boar include crop and infrastructure damage, transmission of diseases to people, livestock and other wildlife, and traffic accidents. Moreover, high densities of wild boar can pose significant threats to biodiversity conservation in sensitive areas (Ballari and Barrios-García, 2014). Generating accurate population dynamics predictions is key to inform decisions about the timing, scale and type of management interventions to prevent or mitigate the negative impacts of this species. This is particularly important in Europe, where wild boar numbers and range have steadily increased in the last decades (Massei et al., 2015).

Compared to other ungulates, wild boar are particularly difficult to manage because of their ecological plasticity and relatively high reproductive rates (Cutini et al., 2013; Fernández-Llario and Carranza, 2000; Fonseca et al., 2011; Giménez-Anaya et al., 2008; Sáez-Royuela and Tellería, 1987). Boar are omnivorous and adapt their diet to locally available resources, with 86 %–96 % of plant (mostly tree seeds, bulbs and crops) and 10 %–20 % of animal and fungi matter (Ballari and Barrios-García, 2014; Giménez-Anaya et al., 2008; Herrero et al., 2006; Massei et al., 1996; Schley and Roper, 2003).

Wild boar prefer dense forest habitats, particularly those formed by mast tree species (Abaigar et al., 1994). However, they occur in almost any type of habitat, including agricultural areas, and more recently in urban environments, where they have access to highly nutritional anthropogenic food (Cahill et al., 2012; Castillo-Contreras et al., 2021; Meriggi and Sacchi, 2001).

Precipitation and temperature, particularly in spring and summer, have been described as key factors affecting wild boar population dynamics in southern Europe. Nevertheless, studies are not unanimous on the role of climate, and factors reported as significant include spring and summer precipitation, (Bisi et al., 2018; Frauendorf et al., 2016), summer temperatures (Focardi et al., 2008; Uzal Fernandez and Nores, 2004) and winter temperatures in colder regions (Borowik et al., 2013).

Climate can impact wild boar dynamics in several ways. For instance, drought can directly affect piglet survival, as piglets have high water requirements during early development (England, 1986; Fernández-Llario and Carranza, 2000; Fraser and Phillips, 1989; Phillips et al., 1990) and dry conditions that harden the soil can make rooting more difficult for all ages, thus reducing food accessibility (Massei et al., 1997).

Weather conditions can also indirectly affect female fecundity. Studies undertaken in Italy and Spain found that spring and summer drought lead to a decrease in the percentage of breeding females (Fernández-Llario and Carranza, 2000; Massei et al., 1996; Sáez-Royuela and Tellería, 1986). Additionally, the effect of climate on the availability

of food, such as acorns, affects directly female body weight and litter size (Fonseca et al., 2011; Gamelon et al., 2013; Massei et al., 1996; Mauget, 1972; Rosell et al., 2012). In northern regions (with cooler summers, and barely limited water availability), spring and winter temperatures, snow cover, forest cover and acorn availability appear to have the most pronounced impacts on wild boar dynamics (Borowik et al., 2013; Geisser and Reyer, 2005; Heptner et al., 1988; Jędrzejewska et al., 1997; Melis et al., 2006; Oloff, 1951). Gethöffer et al., 2007, 2023 also showed that precipitation during May and July, together with the number of frost days in February affect wild boar female weight, which is directly related with the reproductive output.

Masting events are another factor adding complexity to food availability and wild boar dynamics. Masting events are the highly synchronous production of seeds by various tree species (mostly oak, *Quercus* sp. and beech, *Fagus* sp. in southern Europe) that result in a sudden increase in the availability of high-energy food which directly influence female body weight, especially in forest habitats (Gethöffer et al., 2023). These resources affect the population dynamics of many ungulate species and of wild boar in particular as this species, unlike other ungulates, is a monogastric and depends on consuming high-energy food for its survival (Barrere et al., 2020; Bieber and Ruf, 2005; Gamelon et al., 2021).

In Mediterranean landscapes the spatial habitat distribution plays a key role for wild boar occurrence (Bosch et al., 2012; Markina-Lamonja, 1998). Wild boar occur more frequently in areas with forest fragments adjacent to large forests and near mountains or riparian woodlands (Giménez-Anaya et al., 2008; Herrero et al., 2006; Virgós, 2002; Acevedo et al., 2006). However, the availability of farmland provide an alternative food source when food is scarce (Abaigar, 1992; Herrero et al., 2006; Sáenz de Buruaga, 1995).

Studies on the effect and extent of density-dependent processes on wild boar population dynamics have reached different conclusions. Some studies suggested that density can influence female body weight, reproductive success and thus population growth (Bruinderink and Hazebroek, 1995; Imperio et al., 2012; Vetter et al., 2015), while other have not found any density-dependence effect on wild boar population growth, fertility or litter size (Choquenot, 1998; Frauendorf et al., 2016; Ditchkoff et al., 2012). Other studies argued that food availability is not regulated by wild boar consumption, as in classic herbivore-plant systems, but it depends on external factors with stochastic variations, hence for this species this density-independent variability would be more prominent than density-dependent processes (Choquenot, 1998; Uzal Fernandez and Nores, 2004).

Most studies on wild boar dynamics have relied on short time series of a single site or on-site comparisons within a single year. However, long-term studies would be ideal for assessing the role of multiple factors on wild boar population dynamics.

The main aim of this study was to investigate the drivers of wild boar demography (population density and growth rate) in 14 sites in a Mediterranean region, where 23 years of wild boar density data are available. This enabled a more robust analysis of wild boar population dynamics with covariates that vary in both time and space and encompass diverse habitats and climate conditions.

Based on the previous studies and knowledge of the populations we formulated four main hypotheses:

1. Wild boar population densities are positively associated with forest cover and habitat diversity.
2. Increased precipitation during spring and summer may lead to higher availability of food resources and survival, resulting in higher population density and growth rate.
3. Female wild boar with higher body weight have better reproductive success, higher survival rates, and higher recruitment rates, leading to higher population density and growth rate.
4. As wild boar densities are still growing, density-dependent processes are unlikely to be a key factor in affecting wild boar population dynamics.

2. Materials and methods

2.1. Study area

The study was conducted in 14 sites spread throughout Catalonia (NE Spain) (Fig. 1). These sites represent a variety of climatic and habitat typologies in the region (Table 1).

2.2. Data collection

2.2.1. Wild boar population data

The wild boar population data used in this study were provided by the Catalan Wild Boar Monitoring Program. Data on wild boar densities were obtained from driven hunts from 1998–1999 to 2020–2021 (23 years), for this study, data from 14 study sites across the Catalan territory with long series (a minimum of 15 years) on wild boar density was used. In total there were 290 yearly estimates of wild boar density across

14 sites (Fig. 2).

Density estimations were derived from driven hunts data which include date, number of hunters and dogs, number of wild boar culled, and number of wild boar observed but not culled. Wild boar density (d) was calculated following the method by (Sáez-Royuela and Tellería, 1988), using the equation:

$$d_{i,t} = \frac{\left(\frac{B_{i,t}}{E_{i,t}} \right)}{A_i}$$

where $d_{i,t}$ is the derived density for location i in year t . B is the number of boar hunted in the location in each study period. E is the hunting effectiveness (calculated as the probability of a wild boar to be culled by:

$E_{i,t} = \frac{\sum_{y=1}^n B_{y,i}/O_{y,i}}{n}$); where B is the is number of wild boar hunted and O the number of boar observed (including hunted and the scaped) for each drive hunt y in year t , and n is the number of observations. A is the surface area (km^2) of the given hunting location.

A total of 290 yearly density estimates were included in the analysis. Density estimates based on hunting bags are often used for monitoring wild boar population trends (Gamelon et al., 2012; Keuling et al., 2018; Massei et al., 2015). The density calculation used in this paper, is also based on hunting bags, but includes a correction for the hunting efficiency (wild boar hunted/wild boar observed). (Acevedo et al., 2009; Segura et al., 2014) showed that hunting effectiveness is highly dependent on local landscape structure parameters and hunters experience among others; thus correcting for hunting efficiency is key to obtaining more precise population estimates particularly when comparing different areas where the conditions can vary (Acevedo et al., 2009;

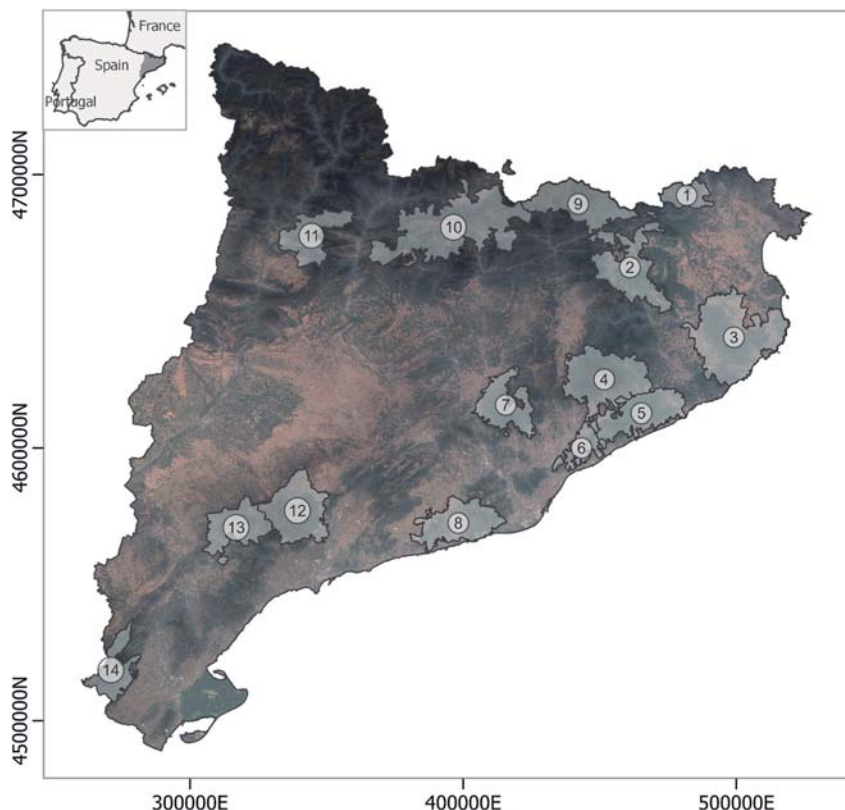


Fig. 1. Location of the 14 study sites of the Catalan Wild Boar Monitoring Program included in the analysis.

Table 1

Characteristics of the 14 study sites included in the analysis. Yearly rainfall and monthly temperatures correspond to the mean of the last 10 years recorded in the nearest meteorological station (data from the Servei Meteorològic de Catalunya).

Sites	Area (ha)	Altitude range (m.a.s.l)	Yearly rainfall (ml)	Mean temp. cooler month (°C)	Mean temp. warmer month (°C)	Wild boar density first monitoring season (wild boar/km ²)	Wild boar density 2021–2022 (wild boar/km ²)
1. Alt Empordà	13.0	53–1.451	647.6	7.7	24.0	16.4	17.5
2. Zona Volcànica de la Garrotxa	41.7	136–1.513	866.1	5.4	22.7	6.4	15.9
3. Gavarres	70.6	0–532	516.5	7.3	24.1	4.5	12.9
4. Montseny	40.7	61–1.706	912.8	1.2	20.6	4.1	14.9
5. Montnegre-Corredor	33.6	0–760	580.6	8.2	23.9	3.0	15.1
6. Serralades Litoral i de Marina	12.9	11–536	581.2	7.5	24.8	3.3	10.5
7. St. Llorenç del Munt	23.8	148–1.103	586.8	6.6	24.0	1.7	7.2
8. Garraf-Olèrdola-Foix	30.2	0–657	635.9	7.3	23.7	2.9	5.9
9. Freser-Setcases	21.5	404–2.909	1031.9	2.2	18.9	3.8	6.1
10. Cadí	26.8	603–2.648	569.4	0.3	18.4	1.0	2.6
11. Boumort	10.8	501–2.077	527.7	2.6	24.7	2.0	4.6
12. Muntanyes de Prades	33.9	118–1.200	485.8	6.0	23.4	2.4	5.8
13. Montsant	29.6	79–1.163	426.6	5.2	24.6	1.2	4.2
14. Ports de Tortosa i Beseit	28.8	163–1.441	648.8	9.4	24.9	1.8	2.2

Segura et al., 2014).

Moreover, recent comparison with other density estimation methods based on camera trap, such as the Random Encounter Model (Chauvenet et al., 2017; Rowcliffe et al., 2008) carried out in the Montseny Natural Park, provided similar density estimates (Minuartia, 2020), strengthening the reliability of the method based on culling and hunting efficiency.

Population growth rate (r_t) was calculated in this study as the log difference in densities of two consecutive years (Roos et al., 2022; Royama, 1992), using the equation:

$$r_{t,i} = \ln(d_{t,i}) - \ln(d_{t-1,i})$$

where $r_{t,i}$ is the proportional growth rate in densities from year $t - 1$ to year t in hunting area i .

2.2.2. Meteorological data

For each of the 14 study sites, meteorological data were obtained from the closest available meteorological station (11 were located within the sites, 2 were within 5 km and the furthest station from a site was 11.6 km). Daily data on precipitation, mean, maximum and minimum temperature, solar radiation and relative humidity were provided by the Catalan Meteorological Service, for the period 01/01/1998–31/12/2021. Variables included in the analysis were seasonal, for easier interpretation, with seasons defined as winter (January, February and March); spring (April, May and June); summer (July, August and September) and autumn (October, November and December).

2.2.3. Landscape data

Landscape variables included in the model (Percentage of forest cover and crop cover) were obtained from the land use and cover cartography elaborated by the Cartography and Geology Institute of Catalonia [ICGC] (1987 a 2002) and the Teledetection and Geographical information system research group [Grumets, CREA-F-UAB (2007 a 2017)] using the R package 'LandscapeMetrics' (Hesselbarth et al., 2019).

2.3. Conceptual framework

Prior to data analysis, we established a conceptual framework, or Directed Acyclic Graph (DAG) (Digitale et al., 2022; Ethier and Nudds, 2017) for an initial consideration of the potential relationship between the different factors affecting wild boar population dynamics. In the conceptual framework we included climate (temperature and precipitation) and landscape (such as altitude, forest cover, crop cover, and habitat diversity) factors that may have an indirect effect mainly through resource availability that in turn may influence population reproduction and mortality. Immigration, emigration, and density dependence processes were also included (Fig. 3).

2.4. Data analysis

Statistical analysis was performed using Generalized Additive Mixed Models (GAMM) to explore the associations of weather conditions, landscape characteristics, and density-dependent processes on wild boar density and population growth rate. A GAMM is a flexible and non-linear regression technique for modelling complex relationships without relying on a predefined functional form, as it allows the estimation both linear and non-linear relationships by using non-parametric smoothing (Murase et al., 2009; Schimek, 2000).

Before running the models, we used Pearson correlation coefficient to measure the linear dependence between two variables. The threshold coefficient was set to ≥ 0.6 but none pair of variables exceeded this value (Zuur et al., 2010).

Two models were run, each using different response variables. The first included derived wild boar population density (wild boar/km²) as the response variable and was modelled as a log-Gaussian distribution (whereby densities were assumed to be strictly positive). We included weather conditions (seasonal precipitation from current and previous year and temperature from previous year), landscape characteristics (forest cover, crop cover), and population variables (female weight previous year) as fixed effects in the model. The model included both site and year as random effects. The model included the following 15 predictor variables (See Supplementary Materials, Tables S1 and S2): current year winter precipitation ($WP_{t,t}$), previous year winter precipitation ($WP_{t,t-1}$), current year spring precipitation ($SP_{t,t}$), previous year spring

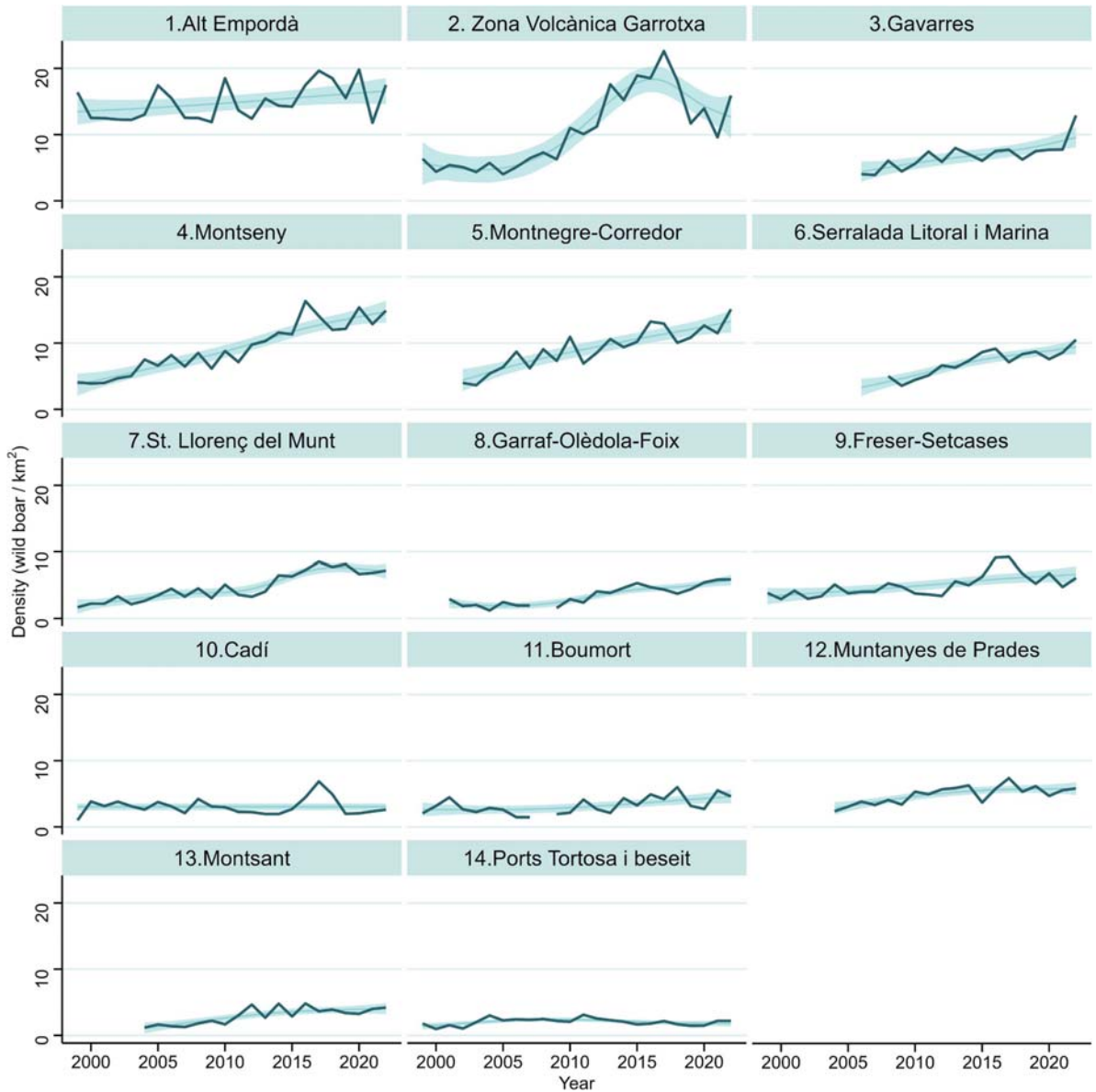


Fig. 2. Wild boar density series for the 14 study sites of the Catalan Wild Boar Monitoring Program included in the analysis. Shadowed in blue are the trends fitted with *Generalized Additive Mixed Models* with 95 % Confidence Intervals for visual aid, the assumptions of the models had not been checked.

precipitation ($SP_{i,t-1}$), previous year autumn precipitation ($AP_{i,t-1}$), current year summer precipitation ($UP_{i,t}$), previous year summer precipitation ($UP_{i,t-1}$), current year total precipitation ($YP_{i,t}$), previous year winter temperature ($WT_{i,t-1}$), previous year spring temperature ($ST_{i,t-1}$), previous year summer temperature ($UT_{i,t-1}$), previous year autumn temperature ($AT_{i,t-1}$), percentage crop surface ($CS_{i,t}$), percentage forest surface ($FS_{i,t}$), previous year female weight ($FW_{i,t-1}$). The model also included 2 random factors (site; Z_i s and year; Z_y) and was based on a sample of 228 observations. Autumn precipitation of the current year was not included as the density is estimated in autumn and there is no time for the autumn precipitation to have any effect. The model was fit using the form:

$$d_{i,t} \sim \text{Normal}(\mu_i, \sigma)$$

$$\begin{aligned} \log(\mu_i) = & \beta_0 + f(WP_{i,t}) + f(SP_{i,t}) + f(UP_{i,t}) + f(WP_{i,t-1}) + f(SP_{i,t-1}) \\ & + f(UP_{i,t-1}) + f(AP_{i,t-1}) + f(YP_{i,t}) + f(WT_{i,t-1}) \\ & + f(ST_{i,t-1}) + f(UT_{i,t-1}) + f(AT_{i,t-1}) + f(CS_{i,t}) + f(FS_{i,t}) \\ & + f(FW_{i,t-1}) + f(YP_{i,t}, CS_{i,t}) + Z_i s + Z_y y \end{aligned}$$

In the second model, the response variable was population growth rate ($r_{i,t}$), modelled as a Gaussian distribution. The same variables used in the first model were included in this model, except for wild boar density at time $t - 1$ that was included as a covariate to assess the association with growth rate at time t , to account for 1st order density-

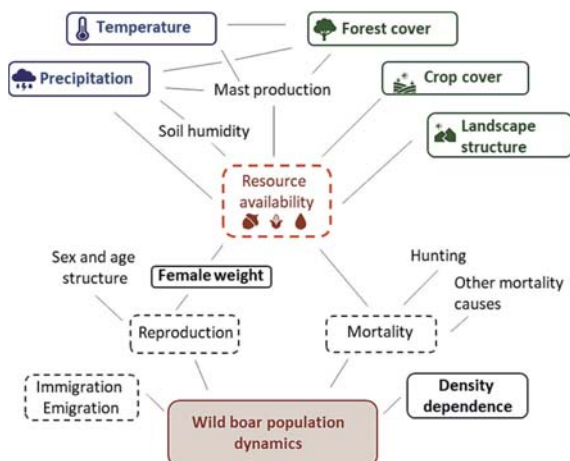


Fig. 3. Simplified conceptual framework, depicting possible associations of the different drivers of wild boar population dynamics. Bold font indicates factors which we had data for and were included in the analysis.

dependent processes. The model included 15 predictor variables, 2 random factors (site and year) and was based on a sample of 201 observations. The variables were the same as in the density model except for the inclusion of previous year density and the dropping of yearly precipitation.

Within both GAMMs, for variable selection we included a penalty on the null space of the basic functions (via the ‘select = true’ argument in the GAMM function in R) to shrink the terms towards zero, if valid, to prevent overfitting and reduce the complexity of the smooth terms (Marra & Wood, 2011). By setting select = true model selection method, we utilized likelihood-based procedures conceptually, similar to variable selection with Akaike Information Criterion (AIC) and the Bayesian Information Criterion (BIC) to identify the most suitable model that balances goodness of fit with model complexity. This model selection process is essential for ensuring that the chosen GLMM accurately captures the relationships within the data, particularly in the context of ecological research where the selection of predictors is a critical aspect of model development. Relevant variables were selected through visual inspection of the smooth plots, further enhancing the model’s validity and interpretability. Model assumptions, such as overdispersion and residual plots, were checked to ensure the validity of the model. For both models assumptions were considered to be met (see Supplementary materials, Figs. S1 and S2). Restricted Maximum Likelihood (REML) was used to estimate the variance components in the mixed model, ensuring unbiased estimates of the parameters. Cubic regression splines were used for constructing smooth terms. Maximum number of knots were set to 10. To assess autocorrelation of population growth rate, we employed the autocorrelation function (ACF). In our analysis, no significant autocorrelation in the ACF plot (Supplementary materials Fig. S3) was detected, indicating that the population growth at a given time point is not strongly correlated with its immediate historical values. All GAMM analyses were carried out in R 4.51.1 (R Core Team, 2022) ‘mgcv’ version 1.8–33 (Wood, 2023).

3. Results

The wild boar density GAMM model had a good fit with the data, with 94.1 % of the deviance explained. Spring precipitation and previous year spring precipitation had both a clear positive, linear effect on wild boar density, with higher wild boar densities associated with higher precipitation during the spring months (March, April and May) of current and previous year. Mean winter temperature of previous year had a

significant non-linear effect, with a positive effect until a threshold around 7 °C; beyond this, the effect transitions into a slightly negative trend. Mean female weight of the previous year showed a significant positive effect, with a stronger effect at the lower weight range, from 33 to 43 kg. The percentage of forest cover also showed a significant association, with a notable positive relationship above 60 % of forest cover (Fig. 4, and supplementary materials Fig. S4).

The population growth GAMM model had a lower fit with the data, with 65.8 % of the deviance explained. The four variables significant for the density model (spring precipitation, previous year spring precipitation, previous year female weight and forest cover), were also significant in the growth model, with similar patterns. Moreover, density had a significant negative effect and previous year summer precipitation was also found as a relevant factor with a non-linear effect with a positive trend above 200 mm of total rainfall (Fig. 5, and supplementary materials Fig. S5).

4. Discussion

By evaluating the main drivers of wild boar density and population dynamics, this research offers an in-depth understanding of the associations between meteorological, habitat and population factors on wild boar populations density and growth in Mediterranean ecosystems.

The results of the analyses indicate that spring precipitation (both from current and previous year), forest cover and female body weight are strongly associated with both wild boar densities and population growth. Summer precipitation and density of the previous year also appear to play a role in population growth. Moreover, density-dependence was detected and it may also play a relevant role in population dynamics.

In particular, spring precipitation and previous year spring precipitation were detected to be positively associated with both response variables (density and population growth) suggesting that drought conditions during the spring months may be a key limiting factor for wild boar, as hypothesized. This relationship could be attributed to increase of food and water availability, leading to higher reproductive output, in terms of proportion of females reproducing and litter size, and higher piglet survival. The positive influence of previous year spring precipitation on wild boar density may be attributed to the heightened availability of food resources. Increased spring precipitation leads to a greater of mast and plant biomass production (Cutini et al., 2013; Espelta et al., 2008), which contributes to higher female body weight, and an increase of the reproductive output. These findings align with prior research conducted in southern Europe, which established that the number of rainy days during spring is a limiting factor for wild boar populations (Uzal Fernandez and Nores, 2004). This is also supported by the fact that our results show the association between mean female body weight from the previous year with both density and population growth, as hypothesized. The positive relationship between female body weight and reproductive output (and thus, population growth potential) has been described in previous papers on wild boar (Aumaitre et al., 1982; Cellina, 2008; Frauendorf et al., 2016; Lombardini et al., 2014; Maugé, 1972; Rosell et al., 2012). Moreover, changes in food availability can also affect on the timing of mating, the age of puberty and the sex ratio of the offspring, which in turn affect population dynamics (Cachelou et al., 2022; Drimaj et al., 2020; Malmsten et al., 2017; Malmsten and Dalin, 2016).

Conversely, the positive association of spring precipitation in the current year on population density could be explained through effects on survival, especially of younger individuals. Given that the majority of wild boar birth occur during March and April (Fonseca et al., 2011; Rosell et al., 2012), moisture content of soil during spring plays a crucial role in facilitating piglet foraging and access subterranean food resources once they are weaned. Low rainfall can prevent access to these food resources and subsequently negatively affect piglet survival (England, 1986; Fernández-Llario and Carranza, 2000; Fraser and Phillips,

Density GAM

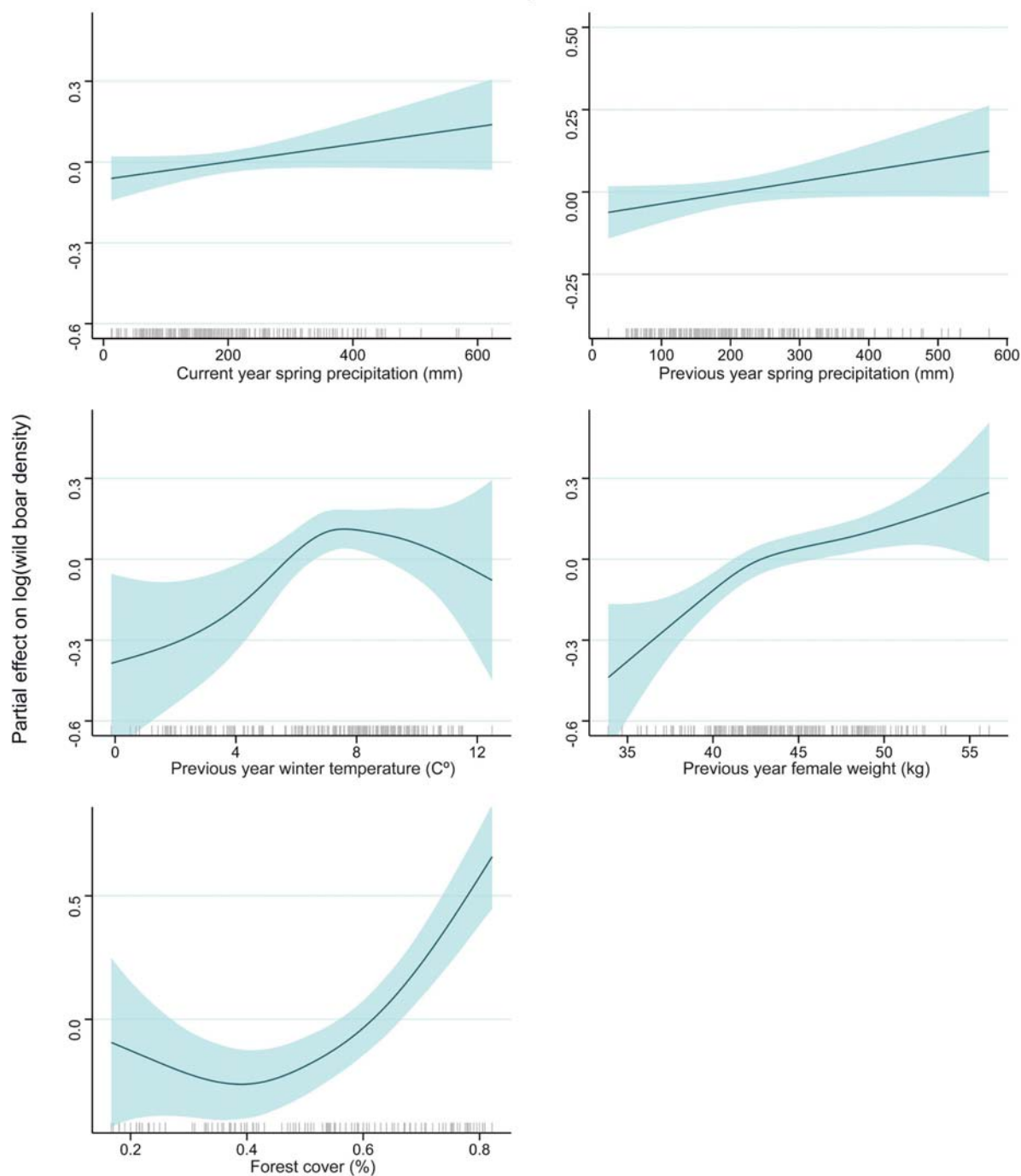


Fig. 4. Effects of selected factors on wild boar density (expressed as the partial effect on log₁₀ density) in Catalonia derived from the results of generalized additive mixed models (GAMMs). The distribution of explanatory variable values is marked with grey vertical lines on the x-axis. The y-axis shows the predicted value of the response variable for a given predictor variable, while holding all other predictor variables at their average. Blue shadow represents the 95 % confidence intervals.

Growth rate GAM

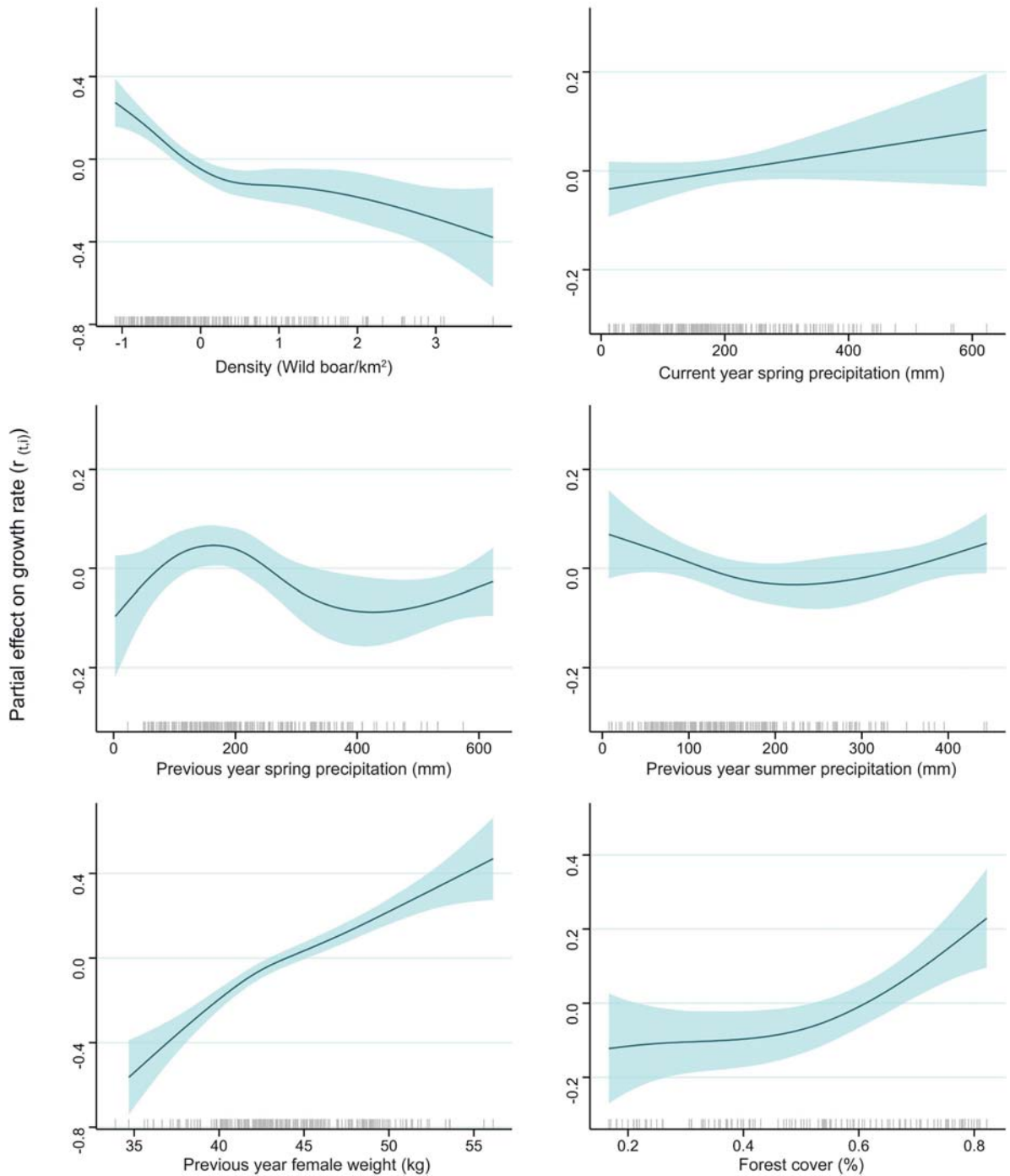


Fig. 5. Effects of selected factors on wild boar population growth rate ($r_{t,i}$, expressed as the partial effect on growth rate), in Catalonia derived from the results of generalized additive mixed models (GAMM). The distribution of explanatory variable values is marked with grey vertical lines on the x-axis. The y-axis shows the predicted value of the response variable for a given predictor variable, while holding all other predictor variables at their average. Blue shadow represents the 95 % confidence intervals.

1989; Phillips et al., 1990). Additionally, water shortages could reduce female milk production, thereby reducing piglet survival during the initial weeks of life, as demonstrated in other ungulates (Cain III et al., 2006).

These results imply that spring precipitation plays a key role in wild boar population dynamics in Mediterranean areas. Given the predicted decrease in precipitation levels in these regions over the next decades (Zittis et al., 2019) due to global warming, this may limit wild boar populations in drier areas and cause a shift of populations to higher and wetter areas within the region. However, wild boar residing in the proximity of agricultural and urban areas may increasingly rely on anthropogenic food (such crop and urban waste), thus making their energy requirements independent of weather conditions. This, in turn, will lead to an escalation of human-wild boar conflicts.

In terms of habitat composition, our study identified forest cover as an important variable associated with wild boar density, while crop cover showed no clear relationship. However, the proportion of crop and forest cover are partially mutually exclusive, which might explain why only one of these variables (forest cover) was associated with wild boar density. These results may suggest that forest habitats remain the most favorable for wild boar populations in Catalonia, with a relationship showing a sharp increase in wild boar density when forest cover exceeded 60 %. Similar results were found in previous studies but in more continental climate; for example, Borowik et al., 2013 reports higher wild boar densities in woodland cover above 40–50 %. On the other hand, another study in Poland reported that the number of harvested wild boars was correlated positively to the increasing of maize crops surface (Kopij and Panek, 2016). In Catalonia, the highest densities of wild boar have historically been recorded in large, continuous forests, although it is likely that crops provide an alternative food source, particularly during drought periods or in years of low production of forest fruits.

The population growth model shows a negative relationship between wild boar density of previous year and population growth. This finding implies Catalanian boar have negative density-dependence, where higher densities can limit but not suppress population growth, likely due to intraspecific competition for resources. Negative density-dependent processes have been widely described in other ungulates, such as moose, chamois or deer (Brown, 2011; Capurro et al., 1997; Coulson et al., 2000), and for wild boar (Imperio et al., 2012; Kapota and Saltz, 2018; Vetter et al., 2015). Other studies investigating wild boar dynamics found only weak density dependence, suggesting that this factor is unlikely to limit wild boar population growth (Bieber and Ruf, 2005; Choquenot, 1998; Frauendorf et al., 2016; Vetter et al., 2020), especially at the current stage of wild boar populations in Catalonia, which are assumed to be far from carrying capacity. Uzal Fernandez and Nores (2004) highlighted the apparent contradiction of assuming intraspecific competition for resources in populations that are still increasing in numbers, particularly in species like wild boar, with highly varied diet. Nevertheless, the variability in environmental factors could produce rapid changes in resource availability from one year to another in certain areas, resulting in increased or decreased intraspecific in-situ competition and subsequent density-dependence (Choquenot, 1998; Massei et al., 1997). In temperate climates with high population densities, intraspecific competition increases winter mortality and reduces fecundity rate in ungulates like chamois (*Rupicapra rupicapra*) and roe deer (*Capreolus capreolus*) (Capurro et al., 1997; Coulson et al., 2000). Density dependence can also affect sex ratio when food resources are limited (Frauendorf et al., 2016) and influence the age of sexual maturity and pregnancy rate among ungulates such as red deer (*Cervus elaphus*) (Clutton-Brock et al., 1986; Kruuk et al., 1999), or affect daily activity patterns for red deer, roe deer and wild boar (Ramirez et al., 2021).

One of the limitations of this study was the lack of data on the availability of natural food resources, as there are no consistent records on forest fruit production or other food sources. The second limitation was

the impossibility to use the number of wild boar hunted as an indicator for mortality, as the number of individuals hunted is one of the parameters employed for calculating density and thus could not be included as an explanatory variable. Finally, the complex nature of our models, combined with the relatively limited sample size and number of factors potentially affecting population density and growth poses a risk of overfitting, implying that the models may excessively capture noise of training data, and its performance in new scenarios should be interpreted carefully. So that, our work should be seen as an exploration of the relevant variables for our study area and conditions which may also be relevant in other situations and are worth to be further studied.

In conclusion, our results provide key insights into the effects of climate, landscape and population factors on wild boar population dynamics in Catalonia, with significant implications for wild boar population management. While meteorological factors cannot be directly controlled, our findings will contribute to elaborate more accurate population predictions based on the interaction of different climate variables for local populations in global change scenarios. Accurate predictions are essential for anticipating and planning management strategies, such as adjusting hunting efforts, implementing alternative methods to culling in conflict areas, or identifying key areas for habitat management and conservation.

Moreover, the limitation by spring precipitation shown by our results, which is likely to affect natural resources availability, is predicted to be more important during the next decades as precipitation is predicted to decrease in Mediterranean areas. Due to the high adaptability of this species, the reliance of wild boar on human-related food (such crop, urban waste or domestic animals food) is likely to increase. Anthropogenic food provide wild boar with highly nutritious resources that improve female fitness (Castillo-Contreras et al., 2021) and the reproductive output of the populations (Rosell et al., 2012). Additionally, crops and urban food resources provide a more stable food supply, independent of weather conditions, that may be particularly relevant for populations residing near agricultural and urban areas, thereby increasing the likelihood of wild boar-human conflicts.

Therefore, effective management measures to reduce anthropogenic food availability are crucial for mitigating conflicts and controlling population growth. These measures can include preventing access to anthropogenic trough crop field fencing or other exclusion measures, securing garbage bins and prevent access of wild boar to domestic animal food, contributing to limit reproductive output, which is directly related to female body weight. Habitat management and reducing refuge areas for wild boar in urban areas might also contribute to mitigate potential conflicts. One of the main findings is the density-dependence processes detected, as population density appeared as relevant factor affecting population growth rate in the study area. Finally, further research is needed to investigate the underlying mechanisms which influence these processes, including the potential impact of factors such as predation, diseases, and climate change. This information may help to design proactive and adaptive management strategies to ensure the sustainable coexistence of wild boars and human populations.

CRedit authorship contribution statement

J. Colomer: Writing – original draft, Methodology, Formal analysis, Data curation, Conceptualization. **G. Massei:** Writing – review & editing, Supervision, Conceptualization. **D. Roos:** Writing – review & editing, Validation, Methodology, Formal analysis. **C. Rosell:** Writing – review & editing, Funding acquisition, Conceptualization. **J.D. Rodríguez-Teijeiro:** Writing – review & editing, Supervision, Methodology.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence

the work reported in this paper.

Data availability

The authors do not have permission to share data.

Acknowledgements

This research is based on the data from the Catalan Wild Boar Monitoring Program, funded by the Catalan Government, Barcelona Regional Council (Diputació de Barcelona), Zona Volcànica de la Garrotxa Natural Park and Gavarres consortium. Special thanks to the hunting teams, technicians, rangers and site coordinators that collaborate with the data collection and management. We thank Simon Croft for his contributions on conceptualization and statistical analysis advise and our colleagues from Minuartia who provided valuable contributions that greatly assisted the research.

Funding sources

This work was supported by the 'Pla de Doctorats industrials' of the Catalan Government.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2024.172739>.

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'Reserve effect': An opportunity to mitigate human-wild boar conflicts

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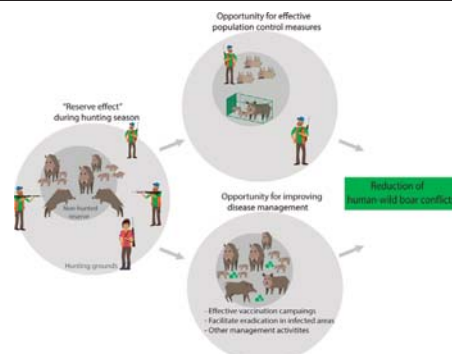
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HIGHLIGHTS

- Wild boar impacts are growing, in parallel with the species' numbers and range.
- Camera traps showed wild boar congregate in reserves where hunting is banned.
- A drastic reduction of wild boar in reserves was observed after a single hunt.
- Population control and disease management can benefit from 'Reserve effect'.
- 'Reserve effect' offers opportunities to mitigate human-wild boar conflicts.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:

Received 13 April 2021

Received in revised form 24 June 2021

Accepted 24 June 2021

Available online 30 June 2021

Editor: Manuel Esteban Lucas-Borja

Keywords:

Population control

Wild boar density

Camera traps

Conflict mitigation

Social organization

Wildlife management

ABSTRACT

Wild boar growth in numbers and range is associated with increasing economic and environmental impact. Hunting has been traditionally used to reduce wild boar numbers. Areas where hunting is not allowed may attract wild boar from neighbouring hunting grounds. This phenomenon is called 'reserve effect' and could cause temporarily localised, high densities of wild boar in areas where hunting is banned. To investigate the occurrence of 'reserve effect', this study was conducted in two natural reserves of 400 and 250 ha inside the Montseny Natural Park, Catalonia, Spain where regular hunting of wild boar is not permitted, and only sporadic driven hunts/year are authorised for population control. The aims of the study were to evaluate if wild boar use these reserves as a refuge when hunting is carried out in the surrounding areas and to assess the effects that occasional drive hunts inside these reserves may have on wild boar numbers and social organization. From 2012 to 2015 camera traps were placed in the two reserves without using any bait. Cameras operated for 1.759 days, including hunting and non-hunting seasons, and 37.574 wild boar images were obtained. A 'reserve effect' was detected, as following hunting in the surroundings grounds, the number of wild boar increases inside reserves. Occasional driven hunts conducted in the reserves are effective in reducing the number of individuals and the effects persist for at least 45 days. Hunting disrupts wild boar social organization, as group size was significantly reduced. These results suggested that targeting refuge areas, once hunting in the surroundings causes wild boar to concentrate in these areas, is effective for population control. These findings could also be used to design strategies to optimise population control and offer opportunities for disease management such as vaccination, or to facilitate eradication in areas affected by disease outbreaks. Crown Copyright © 2021 Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

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1. Introduction

Wild boar occur in a wide range of habitats and climates, have few natural predators and are characterised by high reproductive rates. This has led to a fast populations growth that has increased in recent decades across Europe, resulting in high population densities in many countries (Bieber and Ruf, 2005; ENETWILD consortium, 2019a; Massei et al., 2015; Náhlik and Sándor, 2003; Sáenz-Royuela and Tellería, 1986) and causing a wide range of conflicts with conservation and human activities.

This species has significant economic and environmental impacts such as damages to crops, urban areas and infrastructures (Cai et al., 2008; Ficetola et al., 2014; González-Crespo et al., 2018; Ikeda et al., 2019; Schley and Roper, 2003) and reduction of biodiversity richness and species abundance (Bongi et al., 2017; Calevo et al., 2017; Carpio et al., 2016; Genov and Massei, 2004; Herrero et al., 2005). Wild boar also pose threats to public health and livestock, due to traffic accidents and to transmission of diseases, such as African swine fever (ASF), classical swine fever and foot and mouth disease (González-Barrio et al., 2015; Guberti et al., 2019; Rossi et al., 2015; Sáenz-De-Santa-María and Tellería, 2015). All these impacts have important economic implications as the costs derived from traffic accidents, crop and urban areas damages and the consequences of disease outbreaks can amount to billions of euros (Barrios-García and Ballarí, 2012; Forman et al., 2009; Guo et al., 2016; Halasa et al., 2016).

To mitigate these impacts, wild boar population control is required and supported by wildlife managers, landowners, farmers, and public administrations including health services. Population control is carried out mainly by recreational hunting (e.g., driven hunts, solo hunts, etc.) and to a much lesser extent by trapping. Understanding the factors affecting the species' behavioural response to hunting is crucial to apply effective and evidence-based population control.

In most countries, hunting is the main cause of wild boar mortality (Keuling et al., 2013; Massei et al., 1997, 2015; Nores et al., 2008; Toigo et al., 2008; Virgós, 2002). Hunting affects population size but may also influence spatial, social and temporal behaviour, and in particular home ranges size, habitat use, activity patterns and group composition (Baubet et al., 1998; Keuling et al., 2008; Maillard and Fournier, 2014; Scillitani et al., 2010; Thurfjell et al., 2013; Vassant et al., 1988). When driven hunts are carried out, neighbouring areas where hunting is not allowed may be used as a refuge by wild boar. This phenomenon, known as 'reserve effect' has been described in previous studies (Frank et al., 2015; Grignolio et al., 2011; Sodeikat and Pohlmeier, 2003; Tolon and Baubet, 2010). Understanding how wild boar use these reserves is essential to optimise population control and disease management strategies, particularly when the latter are based on a mosaic of areas where culling may or may not be allowed (Keuling et al., 2018; Tolon et al., 2009). Furthermore, no studies have addressed the impact of driven hunts on wild boar behaviour and numbers inside reserves adjacent to areas where hunting occurs. This is particularly relevant for management of diseases such as ASF that rely on core and buffer zones around the outbreak where culling is temporarily banned, and on an intensive hunting area, surrounding the buffer zone, where culling is encouraged (Jori et al., 2020; More et al., 2018).

As wild boar impact is often associated with local population density, the effectiveness of interventions employed to reduce such densities is based on estimating the number of animals before and after population control has been implemented. Of the methods available to estimate wild boar population density (Engeman et al., 2013), several require significant resources, making their implementation unfeasible. One of the most widespread methods is based on hunting statistics, which allows monitoring of large areas with reasonable costs and staff time (ENETWILD consortium, 2019b; Gamelon et al., 2012). Camera traps can also be used to obtain consistent estimates of populations size (Chauvenet et al., 2017; Keuling et al., 2018; Massei et al., 2017; Minuartia, 2020; Rowcliffe et al., 2008). Moreover, camera trap images

allow to collect data on individual behaviour, social interactions, group composition, reproductive output, activity patterns and responses to human presence and hunting (Erdtmann and Keuling, 2020; Lashley et al., 2018; Oliveira-Santos et al., 2013; Palencia et al., 2019; Rowcliffe et al., 2014, 2016). This study used camera traps to monitor changes in wild boar numbers, group size and composition before and after hunting occurred.

The aims of the study were 1. to evaluate if wild boar use reserves as a refuge when hunting is carried out in the surrounding areas; 2. to assess the effects that occasional drive hunts inside these reserve have on wild boar numbers; and 3. to determine the effects of hunting on wild boar group size and composition. The hypotheses were that i) following hunting in the surroundings grounds, the number of wild boar increases inside these reserves; ii) occasional driven hunts conducted in the reserves are effective in reducing the number of individuals and iii) hunting disrupts wild boar social organization.

2. Materials and methods

2.1. Study area

The study was carried out in the Montseny natural park which covers 31.064 ha and is situated in the Catalan pre-littoral mountain range (NE Spain) 17 km from the coastline, with an altitude ranging from 100 to 1.700 m a.s.l. (Fig. 1). The area is located in the Mediterranean region but at the higher altitudes above 1.000 m, the climate is temperate, creating a marked gradient of climate and vegetation. Average annual rainfall is 1.053 mm. Mean annual temperature at the highest altitudes is 7.1 °C with a maximum monthly mean in July of 15.5 °C and a minimum in January of 1.0 °C. At lower altitudes, mean annual temperature is 14.8 °C with a monthly mean maximum in July of 23.6 °C and a minimum on January with 7.2 °C (Servei Meteorològic de Catalunya, 2016).

Inside the natural park, there are eight areas with special protection known as natural reserve areas (here after NRA), with occupying a total of 2606 ha (8.4% of the total surface of the natural park) where regular hunting is not permitted. This study was carried out in the two largest areas: Matagalls-Sant Marçal-Vall de Riudeteix (hereafter referred as Riudeteix) and Vallforneres, which together occupy 1515 ha.

Riudeteix is situated between 670 and 1.697 m a.s.l and includes an area of 1.117 ha. The vegetation is composed mainly by dense forests dominated by holm oak (*Quercus ilex*) forest, intermixed with beech (*Fagus sylvatica*) and chestnut (*Castanea sativa*) forests. At higher altitudes, the vegetation is dominated by bushes such as junipers (*Juniperus communis* ssp. *nana*) and broom (*Genista purgans*), mesophilic and xerophilous meadows, wet meadows and reedbeds (OTPAT, 2008).

Vallforneres includes an area of 389 ha with a high diversity of habitats situated between 700 and 1.300 m a.s.l. The vegetation is dominated by sclerophyllous species, mainly holm oak, but also conifers and riparian forest, and at the higher altitudes, open habitats dominated by grassland and shrubs as in Riudeteix.

2.2. Hunting data – wild boar monitoring program

In Catalonia a wild boar monitoring program was implemented in 1998, based on data provided by hunting teams at the end of the hunting seasons. Participants deliver a notebook where data from each driven hunt are recorded and include date, number of hunters and dogs, number of wild boar hunted, and number of animals observed but not hunted. These data are used to estimate wild boar density in each of the 22 participant areas in Catalonia. Currently more than 173 hunting groups participate in the program, providing information on about 5.000 hunts each year. The complete database contains data about more than 85.000 driven hunts. These data are analysed to monitor population trends across the whole region, with reports annually published by the Catalan Ministry of Agriculture, Livestock, Fisheries

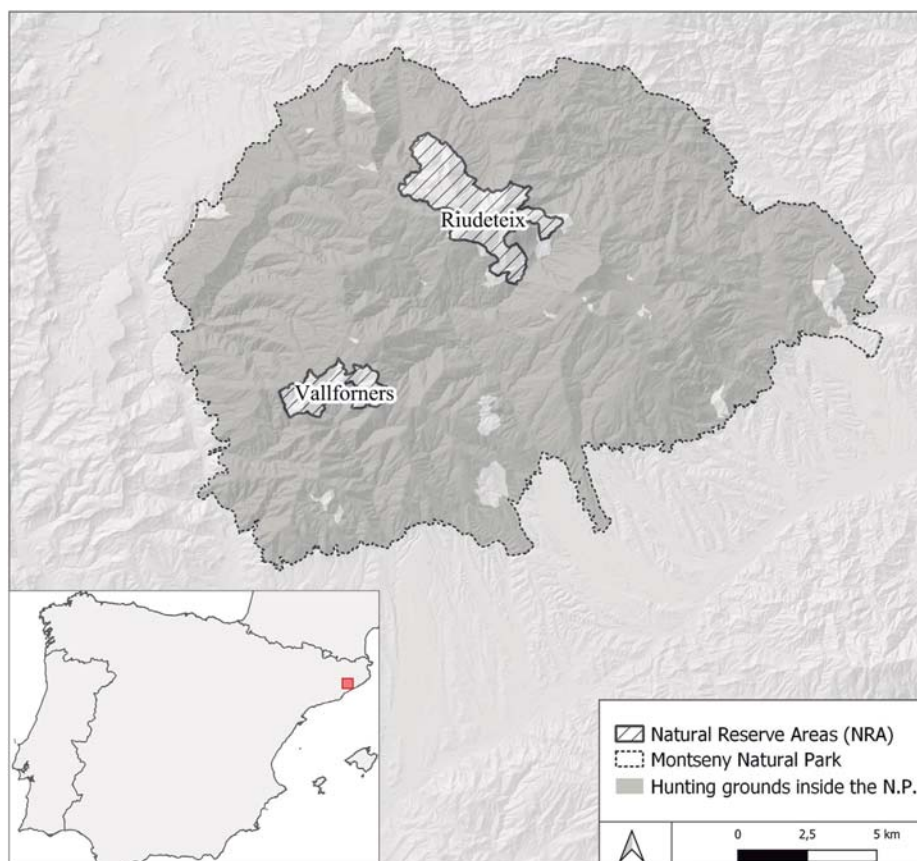


Fig. 1. Location of the two study sites, the Natural Reserve Areas (NRA) of Vallforners and Riudeteix situated within the Montseny natural park, Catalonia, Spain. Hunting areas occupy almost the whole area of the natural park except the NRA and other small sites.

and Food since 1998 (DARP, 2020). Since 1998, Montseny natural park participates to the Catalan Wild boar Monitoring Program.

Two wild boar density indices are calculated each year: 1. a relative density index (Rosell, 1998) which takes into account the total number of wild boar harvested, the hunting effort and the surface of the hunting area and 2. an estimate of the absolute density (Saez-Royuela and Telleria, 1987), considering the ratio of wild boar hunted vs. observed per area (Table 1). These methods are often used for monitoring wild boar trends (Gamelon et al., 2012; Keuling et al., 2018; Massei et al., 2015). Moreover, recent comparison with other density estimation methods based on camera trap, such as the Random Encounter Model (Chauvenet et al., 2017; Rowcliffe et al., 2008) carried out in the Montseny natural park, have provided similar density estimations

(Minuartia, 2020), reinforcing the field operatives' confidence in the method based on hunting data.

During the study period (2012 to 2015) wild boar density estimate by the wild boar monitoring program in Montseny natural park increased from 10 individuals/km² in 2012/2013 to 16 individuals/km² in 2015/2016 (Table 1), the maximum ever registered in the 20 years monitoring period (DARP, 2016).

Throughout the whole natural park, surrounding the two NRA, there was a relatively high hunting pressure during the study periods according to the monitoring program, as on average 110 hunts (SE = 0.95) were carried out each month (from September to February), representing around 1.4 hunts/km². Hunts had a mean participation of 24 (SE = 0.44) hunters and 19 (SE = 0.37) dogs (Table 1).

Table 1

Wild boar density estimates and hunting pressure parameters in the Montseny Natural Park during the study period. Data from the Catalan Wild Boar Monitoring Program (DARP, 2016).

Variable	2012/2013	2013/2014	2014/2015	2015/2016
Wild boar density (individuals/km ²)	10.29	11.59	11.31	16.34
Number of hunts/year/km ²	1.40	1.37	1.33	1.54
Mean number of hunts/month	110.16	107.33	104.00	117.17
±SE	7.10	6.20	5.20	4.12
Mean number of hunters/hunt	23.14	23.61	24.10	24.05
±SE	0.43	0.45	0.45	0.39
Mean number of dogs/hunt	18.79	18.94	18.21	18.02
±SE	0.37	0.40	0.36	0.32

Population control driven hunts were exceptional hunts carried out inside the NRA. These were authorised by the natural park authorities with the objective of culling the maximum number of wild boar inside these areas. These control driven hunts carried out once or twice per year, during the winter months, attracted a higher number of participants, with an average of 31 (SE = 0.58) hunters and 27 dogs (SE = 0.49), compared to regular driven hunts carried out in the surroundings areas.

2.3. Data collection

Camera trapping was conducted to monitor abundance and group composition of wild boar inside the two reserves. No bait was used to attract the animals. Reconyx RC55 and HC500 camera traps were situated in trees next to active wild boar trails.

Five camera trap locations (two in Riudeteix and three in Vallforners respectively) were in operation during the whole period and were considered for the analysis. Camera traps operated for 1759 days (Table 2). Other cameras were placed in the NRA during these years but were not working for the whole period and have not been included in the present study. Nevertheless, the data provided by these extra cameras has been used to check consistency of the results obtained. The same patterns of numbers of individuals inside the reserve are during the hunting and non-hunting season were coincident with the ones observed in the cameras selected for this study. Moreover, the fact that the results obtained in the present paper by the 5 cameras are consistent across the four years of study, together with the high number of day in operation and registers obtained, reinforce the robustness of the dataset and the conclusions that can be drawn.

In Riudeteix two camera traps were placed in an area of 250 ha situated between 875 and 1050 m a.s.l., covered mainly with Mediterranean oak and excluding the higher open areas of the NRA. In Vallforners three camera traps were distributed across the whole area of the NRA, dominated by Mediterranean oak. Cameras were placed in locations without attractive resources for wild boar, in points with conditions and habitats similar to the whole study area. Locations were chosen to assure that camera traps had a good area of vision of wild boar movements, avoiding areas with dense vegetation that interfere in the camera traps range.

2.4. Data analysis

Visual identification was used to define the minimum number of individuals, the age class and group size for each group of wild boar that visited the camera traps. Photographs taken less than 10 min apart were considered the same visit (Massei et al., 2017). Group composition was classified in four categories, matriarchal groups, solitary males, subadults or indeterminate; group size was determined by counting the total number of individuals in each group. Matriarchal groups were described as any group of one or more adult sows with their youngs.

Subadult groups are composed by small number of subadults. Camera traps recorded a sequence of 5 consecutive photos and the minimum time lag between bursts was selected (0.6 s). For each sampling location, the daily mean number of wild boar (minimum count of individuals recorded in the photos taken per day in each camera trap) was calculated. Before any analysis, the autocorrelation between the daily individual counts was tested indicating that each daily observation was independent from the previous and following days.

2.4.1. 'Reserve effect' analysis

To investigate the 'reserve effect', camera traps were used to assess the presence of wild boar inside the reserve areas. The study periods of 2014/2015 and 2015/2016 were selected, since they are the years that present complete camera trap data for the regular hunting and no hunting seasons. The number of wild boar individuals recorded by the camera traps inside the NRA (where hunting is normally forbidden) during regular hunting and non-hunting season in the surroundings areas was analysed. Differences of this variable in each site and season between hunting and non-hunting periods, and before and after the population control hunt, were tested using Mann-Whitney tests. Sequential Bonferroni corrections (Rice 1989), in which alpha was 0.05 (number of years by NRA) were used for the first comparison. Differences in group composition before and after the regular hunting season and before and after the population control driven hunt were tested by chi-square tests. Only the period before the first population control driven hunt inside the NRA was considered, as after the disturbance the NRA could not be considered a hunting reserve anymore.

2.4.2. Population control driven hunt inside the reserves

For testing the effects of the population control driven hunt inside the reserves on wild boar numbers and group composition camera traps were used to assess the number of individuals before and after the hunts. The four study periods in which the camera traps were in operation during the hunting season were considered (2012/2013, 2013/2014, 2014/2015 and 2015/2016). An analysis before / after the hunting control within the reserve was carried out to assess the effect of hunting on numbers and group composition. A period of 45 days after the first population control driven hunt was considered, as previous studies reported that the effects of a driven hunt on wild boar home ranges can be detected during a period of 4 to 6 weeks (Sodeikat and Pohlmeier, 2003). In addition, the present study also tested whether the effects of the population control driven hunt on wild boar numbers and group composition persisted for longer periods, specifically for 60 days, in the instances where data were available.

To evaluate the effectiveness of the population control hunt in decreasing the number of wild boar inside the NRAs, an Interrupted time series analysis (ITS) was carried out. The ITS examined changes in the slope of the trend of daily mean number of wild boar detected/camera

Table 2

Duration of the camera trap monitoring in each NRA during both open hunting season (September to February) and closed hunting season (February to September) in the surrounding areas of the Montseny Natural Park. Two and three camera traps were used in Riudeteix and Vallforners respectively.

Natural Reserve Area	Hunting season	Installation	Removal	Proportion of days in operation
Riudeteix	Hunting 2012/2013	30/10/2012	12/03/2013	82%
	Hunting 2013/2014	06/11/2013	23/02/2014	100%
	Non-hunting 2014	24/02/2014	06/09/2014	100%
	Hunting 2014/2015	07/09/2014	22/02/2015	100%
	Non-hunting 2015	23/02/2015	06/09/2015	99%
	Hunting 2015/2016	06/09/2015	18/02/2016	100%
	Total			97%
Vallforners	Hunting 2012/2013	–	–	
	Hunting 2013/2014	03/10/2013	23/02/2014	81%
	Non-hunting 2014	24/02/2014	31/08/2014	100%
	Hunting 2014/2015	01/09/2014	22/02/2015	76%
	Non-hunting 2015	23/02/2015	05/09/2015	100%
	Hunting 2015/2016	06/09/2015	18/02/2016	100%
	Total			92%

trap/day in each study site during the hunting season in Montseny natural park before and after the population control hunts were carried out inside the reserves (Bernal et al., 2017).

Before the ITS analysis was carried out, data autocorrelation (tendency of observations closer in time to be more similar between each other) and overdispersion (variability greater than the expected by the model) were tested. As the data did not show autocorrelation but tested positive for overdispersion, a Quasi-poisson distribution was used, which allows the variance to be proportional rather than equal to the mean. The ITS analyses were carried out using the script available on Bernal et al. (2017). All data analyses were carried out in R (R Core Team, 2020).

3. Results

3.1. 'Reserve effect'

During 2014/2015 and 2015/2016 seasons, camera traps were in operation for 723 and 724 days respectively (Table 2) and recorded 7800 and 12,908 wild boar images in Riudeteix and Vallforners respectively. Wild boar were detected in all operational camera traps, with an average daily number across sites and seasons of 2.45 (SE = 0.11, range = 0–41) wild boar /day.

Comparison of the number of individuals between regular hunting and non-hunting season, showed that wild boar concentrate in the NRA when hunting occurs in the surroundings areas. The average number of individuals was significantly higher inside the NRA during the hunting season, than the non-hunting season for both years in the Vallforners site (2014/2015: Mann-Whitney U test $W = 4785.5$, $n_1 = 195$, $n_2 = 85$, $P < 0.001$; 2015/2016: $W = 7732$, $n_1 = 193$, $n_2 = 91$, $P < 0.001$) and for the 2015/2016 period in the Riudeteix site (U test $W = 6815$, $n_1 = 194$, $n_2 = 82$, $P < 0.001$), but not for Riudeteix during 2014/2015 ($W = 12,962$, $n_1 = 195$, $n_2 = 131$, $P = 0.811$) (Fig. 2).

For both study sites, the mean group size detected inside the NRA was higher during the regular hunting season than the non-hunting

season for both years in the Vallforners site (2014/2015: Mann-Whitney U test, $W = 3712$, $n_1 = 287$, $n_2 = 151$, $P < 0.001$; 2015/2016: U test, $W = 31,775$, $n_1 = 171$, $n_2 = 185$, $P < 0.001$) and for 2015/2016 in the Riudeteix site (U test, $W = 5715.5$, $n_1 = 163$, $n_2 = 162$, $P < 0.001$) but not for Riudeteix during 2014/2015 ($W = 21,168$, $n_1 = 207$, $n_2 = 151$, $p\text{-value} = 0.576$). Mean group size for each period are reported in supplementary materials (Table S1).

Group composition differed between the non-hunting and the regular hunting season for both sites and study periods after Bonferroni correction (Vallforners: 2014/2015: $\chi^2_3 = 42.90$, $P < 0.001$; 2015/2016: $\chi^2_3 = 55.71$, $P < 0.001$. Riudeteix: 2014/2015: $\chi^2_3 = 32.04$, $P < 0.001$; 2015/2016: $\chi^2_3 = 23.09$, $P < 0.001$). The proportion of matriarchal groups was higher inside the NRAs during the hunting season than during the non-hunting season in all cases. No consistent patterns were observed on proportions of solitary males and subadults across years and sites (Fig. 3).

3.2. Effects of population control driven hunt inside the reserves

During the hunting seasons from 2012/2013 to 2015/2016, two and three camera traps were in operation for 1102 days (Table 2) and recorded 17,532 and 20,042 wild boar images in Riudeteix and Vallforners respectively. Wild boar was detected in all operational camera traps, with an average daily number of individuals across sites and seasons of 2.75 (SE = 0.10, range = 0–41).

The population control driven hunts inside the reserve were carried out once per season except for Vallforners in 2014/2015 and 2015/2016, when two population control hunts were carried out but only the period after the first hunt has been considered for the analysis.

The mean number of wild boar detected/camera trap for a period of 45 days after the population control hunt was lower than that before the hunt for all years in Vallforners (2013/2014: Mann-Whitney U test, $W = 278$, $n_1 = 105$, $n_2 = 45$, $P = 0.001$; 2014/2015: $W = 501.1$, $n_1 = 30$, $n_2 = 45$, $P < 0.001$, 2015/2016: $W = 427.5$, $n_1 = 91$, $n_2 =$

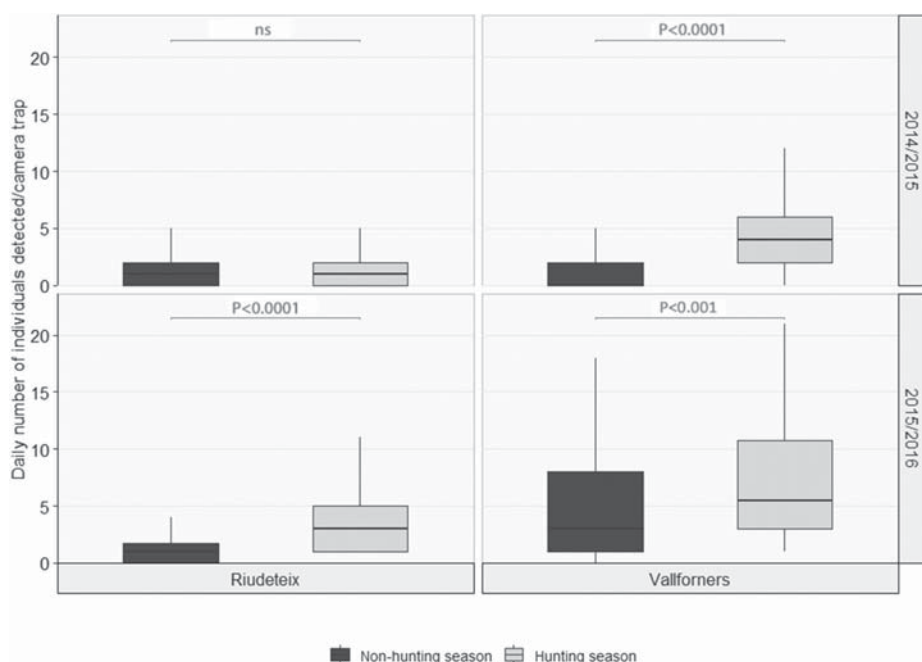


Fig. 2. Daily number of wild boar individuals detected/camera trap inside the NRAs during non-hunting season (spring and summer) and hunting season (autumn and winter) in the Montseny natural park before any population control hunt was carried out inside the NRAs. The line inside the box represents the median, lower and upper box boundaries represent 25th and 75th percentiles respectively and lower and upper error lines; 10th and 90th percentiles respectively. ns: $p > 0.05$.

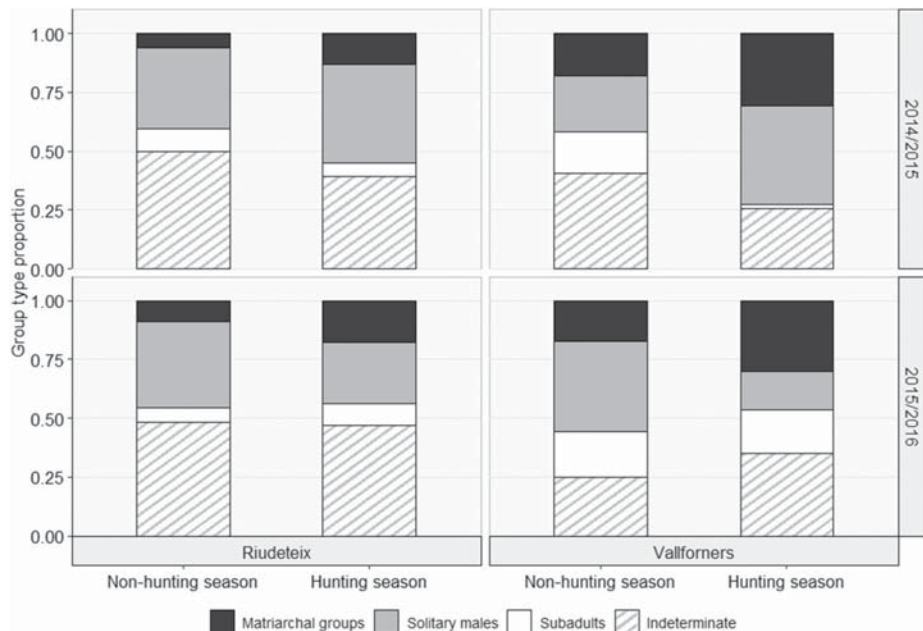


Fig. 3. group composition proportions observed in the two non-hunted study sites during non-hunting and hunting season in the other hunted parts of the Montseny natural park.

45, $P = 0.019$) and for the first three years in Riudeteix (2012/2013: $W = 532.5$, $n_1 = 53$, $n_2 = 45$, $P < 0.001$; 2013/2014: $W = 488$, $n_1 = 152$, $n_2 = 34$, $P < 0.001$; 2014/2015: $W = 1501$, $n_1 = 131$, $n_2 = 42$, $P < 0.001$). Only the 2015/2016 season in Riudeteix the decrease was not significant ($W = 287.5$, $n_1 = 67$, $n_2 = 45$, $P = 0.079$) (Fig. 4). Data of 60 days after the hunt were only available in four cases (Riudeteix 2012/2013 and 2015/2016 and Vallforners 2014/2015 and 2015/2016). In these cases, differences in wild boar numbers before and after the population control driven hunt were significant only in Riudeteix for the season 2012/2013 (Mann-Whitney U test, $W = 651$, $n_1 = 53$, $n_2 = 60$, $P < 0.001$), in all other cases (Riudeteix 2014/2015, and Vallforners 2014/2015 and 2015/2016) differences were not significant (Mann-Whitney U test, $W < 800$, $P > 0.049$).

The interrupted time series analysis showed that the population control driven hunts inside the reserves reduced wild boar numbers and that the effects were still lasting after 45 days (Fig. 5). In all study periods for both sites, the observed trend based on the regression model of individual numbers detected per day was lower than the predicted trend if the intervention had not been carried out.

The effect of single population control driven hunts inside the reserves on group size was not consistent across areas and years (Table S2). At Vallforners, there was a significant decrease in mean group size for all the three seasons (2013/2014: Mann-Whitney U test: $W = 35,355$, $n_1 = 285$, $n_2 = 181$, $P < 0.001$; 2014/2015: $W = 54,655$, $n_1 = 162$, $n_2 = 208$, $P < 0.001$, 2015/2016: $W = 42,640$, $n_1 = 153$, $n_2 = 214$, $P < 0.001$). At Riudeteix, mean group size differed for the 2015/2016 season ($W = 6694$, $n_1 = 109$, $n_2 = 85$, $P < 0.001$) but not for the first three seasons ($W < 22,066$, $P > 0.164$), although the same trend in decreased group size was observed.

Where individual and groups could be identified, consistent but only borderline significant differences in group composition frequencies emerged when comparing the period before the population control driven hunt and the 45 days after the hunt (Fig. 6). No differences were observed in Vallforners (after Bonferroni correction) for all three study periods (2013/2014: $X^2_3 = 9.11$, $P = 0.028$; 2014/2015: $X^2_3 = 10.56$, $P = 0.032$; 2015/2016: $X^2_3 = 6.52$, $P = 0.030$) and in Riudeteix only 2015/2016 ($X^2_3 = 17.98$, $P < 0.001$) was significant after Bonferroni

correction ($X^2_3 < 7.82$, $P > 0.049$). Bonferroni correction is a very conservative test and in all cases the p values were very close to significance.

4. Discussion

This study substantiated the hypotheses that i) following hunting in the surroundings grounds, the number of wild boar increases inside reserves; ii) occasional driven hunts conducted in the reserves are effective in reducing the number of individuals; and iii) hunting disrupts wild boar social organization.

In particular, the study confirmed that when driven hunts, that involve tens of hunters and dogs, are carried out, wild boar seek refuge in reserve areas where hunting is banned. The results also indicated that this behaviour seems particularly apparent in matriarchal groups and that hunting affects group size and composition. This was also the first study that investigated the effects that control driven hunts inside refuge areas have on wild boar numbers and on group composition. Although few camera traps were employed during the study, albeit for consecutive years, the results were reasonably consistent across the two reserves and the years.

The 'reserve effect' for wild boar was detected in this study, similarly to what described in previous studies (Amici et al., 2012; Rosell et al., 2004; Tolon et al., 2009; Tolon and Baubet, 2010). Amici et al. (2012) found that the presence of non-hunted areas close to cultivated areas was a significant factor affecting crop damage by wild boar, supporting the hypothesis of a 'reserve effect'. Tolon et al. (2009) showed that wild boar moved to the reserve during the open hunting season but also that there was a threshold distance (2.1 km) beyond which animals did not respond to hunting disturbance as they might have not perceived the safety in the reserve. As the two reserves in the present study are more than 5 km apart, it is likely that the wild boar attracted to one of the reserves were not affected by the other one. Rosell et al. (2004) found the maximum number of wild boar in the non-hunted reserves in a wetland area during the autumn months, which coincided with the start of the hunting season in the surroundings. This also coincided with the lack of food resources in the neighbouring areas, which were

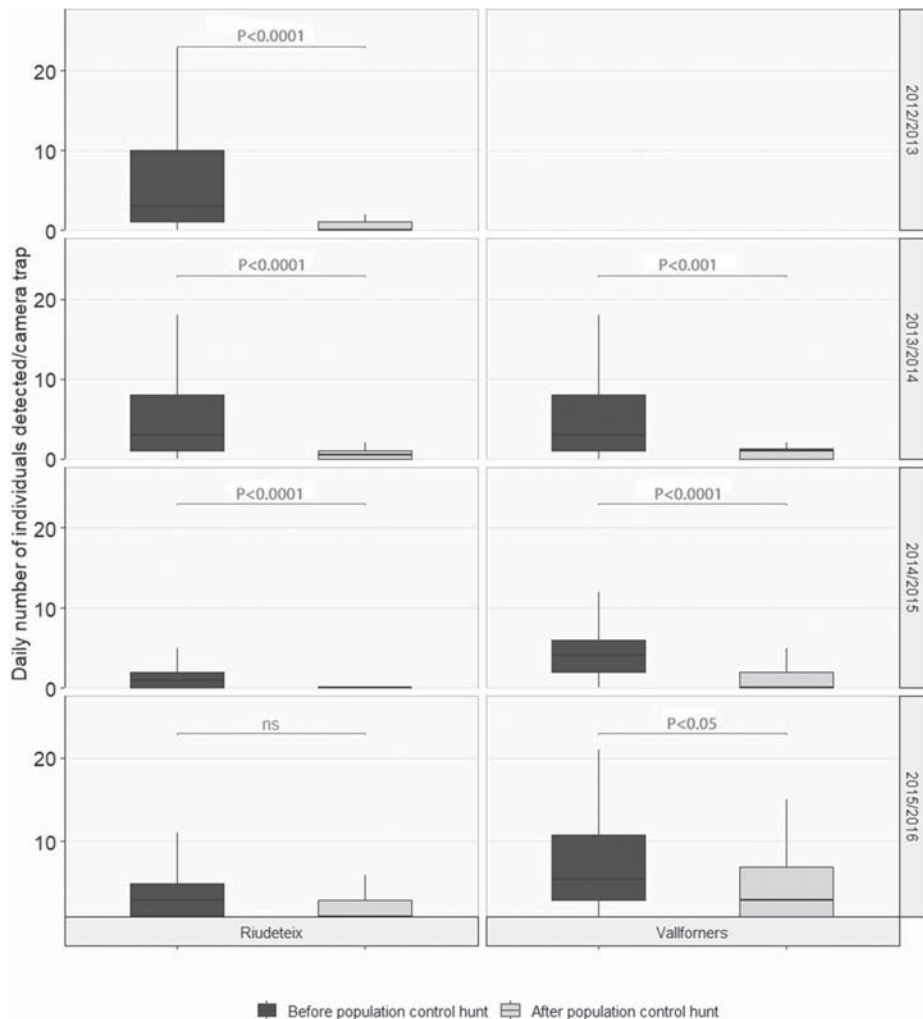


Fig. 4. Daily number of wild boar detected/camera trap during the hunting season in Montseny natural park before and 45 days after the population control hunts in each site and study period. The line inside box represents the median, lower and upper box boundaries represent 25th and 75th percentiles respectively and lower and upper error lines; 10th and 90th percentiles respectively. ns: $p > 0.05$.

occupied mainly by cereal crops harvested at the end of summer and might have encouraged wild boar towards the reserves where food resources are available during autumn and winter. The same study also observed larger group size during the mating season which coincided with the hunting season. The present study showed that group size and proportion of matriarchal groups increased significantly inside the reserves during the hunting season (autumn and winter). These variations could be due to both the hunting pressure but also to seasonal variations in social organization at the beginning of the mating season as in Rosell et al. (2004).

A 'reserve effect' has also been described for other ungulate species, for instance roe deer (*Capreolus capreolus*) sought refuge in protected areas when hunting with dogs was conducted in the surroundings, even though this species was not targeted by these hunts (Grignolio et al., 2011). Similarly, farmland (Casas et al., 2009) and wetland birds species (Bregnballe and Madsen, 2004; Madsen, 1998) during the hunting season switch their resting areas to sites where hunting is banned.

Conversely, Brogi et al. (2020) did not find any evidence of 'reserve effect' in wild boar and attributed the increased number of animals in

a non-hunted areas during autumn to the presence of food resources inside these areas. In the present study, food resources appeared equally distributed as there is the same type of habitat, dominated by holm oak, intermixed with beech and chestnut forests inside and outside the reserves. The increase of wild boar numbers was very likely due to the safety that non-hunted areas offered during the hunting season, as partly indicated by the sudden shift in numbers once the hunting season had started.

Where the 'reserve effect' occurs, adaptive management is required to achieve population reduction objectives across a whole area. For this reason, one or two control driven hunts per year were authorised inside the NRAs in Montseny natural park where hunting is normally banned. This study confirmed the hypothesis that these occasional hunts are effective in decreasing number of wild boar in the reserves. The effect of these hunts persisted for at least 45 days, in agreement with previous studies that showed that after a single hunt wild boar returned to their original home ranges within four to six weeks (Sodeikat and Pohlmeier, 2002). The reduced numbers of wild boar inside the reserves post-occasional driven hunts could be due to a combination of

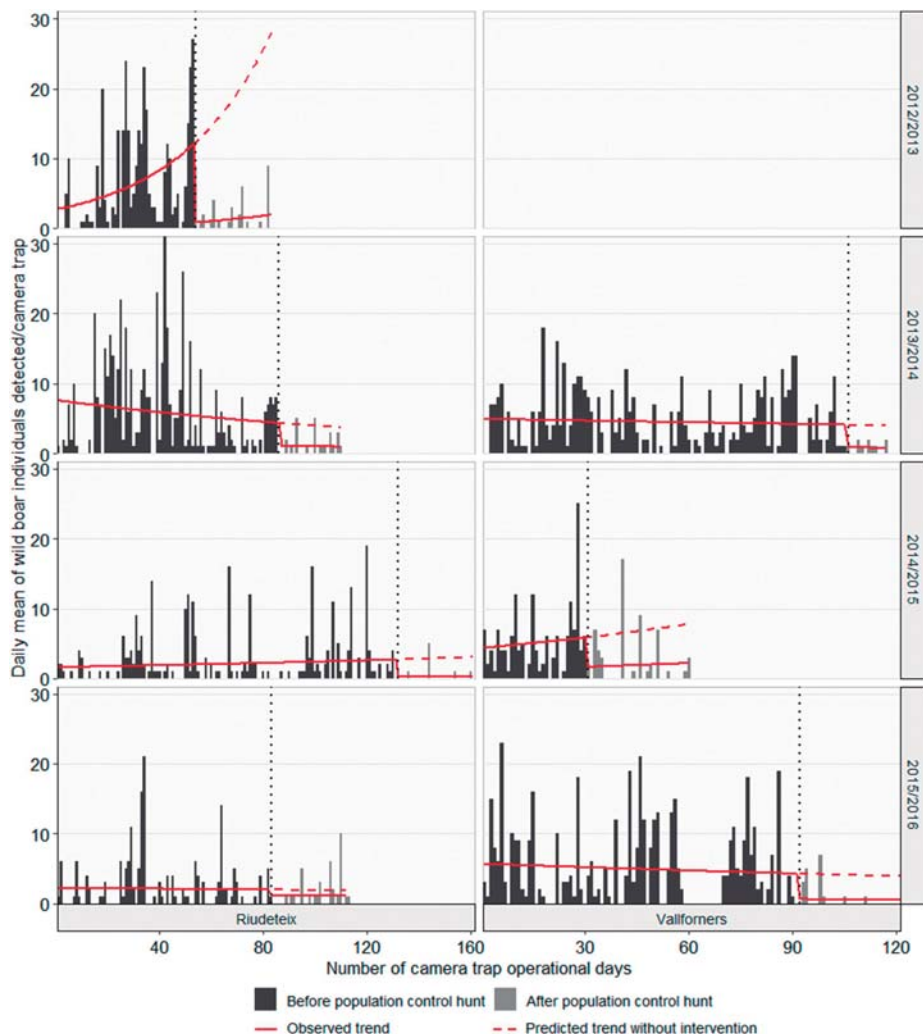


Fig. 5. Daily mean number of wild boar detected/camera traps in each site and study period during the hunting season in Montseny natural park before and after the population control hunts (represented by vertical black dotted lines) were carried out inside the reserves. Solid lines show the actual trend before and after the driven hunt. Dashed lines show the predicted trend based on regression model if the population control hunt had not been carried out. The 'after' period includes 45 days after the population control hunt.

individuals that have been culled and animals that emigrated outside the reserves. Spatio-temporal variations of risk perception are major drivers of animal distribution especially for intensely preyed upon or harvested species responding to the so called "landscape of fear" (Brown et al., 1999; Thurfjell et al., 2013; Tolon et al., 2009). Future studies using camera traps inside and outside the reserves to estimate wild boar numbers throughout the year should establish whether the persistent decreased number of wild boar inside the reserves, following a single hunting event, is due to numbers removed by hunters, to emigration or to both.

The results show that single driven hunts carried out inside the reserves resulted in a decrease of group size. This may be caused by loss of individuals that have been culled but also from group disruption or individuals leaving the original groups. Previous studies found that hunting, even a single driven hunt affects social behaviour, activity patterns and spatial use (Keuling et al., 2008; Maillard and Fournier, 2014; Miguel et al., 2020). Nevertheless, the effects caused by hunting on wild boar social organization are uneven across sites and different studies do

not agree on how wild boar respond to hunting (Massei et al., 2011; Podgórski and Śmietanka, 2018).

Group composition was only affected by population control driven hunts inside the reserves in one case, for Riudeteix in 2014/2015, when the proportion of matriarchal groups decreased while that of solitary males and subadults increased. This tendency was observed in all the other study cases, although the difference was not significant. These variations could be partly explained by regular season variations in group compositions. However, previous studies showed that the proportion of matriarchal groups during autumn and winter remain stable (Rosell et al., 2004), while the results of the present study show that there was a significant decrease during these periods in both study sites, supporting the idea that the hunting intervention was the cause of the severe reduction of the number of matriarchal groups observed. The fact that matriarchal groups decrease after disturbance can be attributed to these groups being more easily hunted as they are more detectable by hunting dogs, but also to the leading sows being more cautious and having a lower threshold of risk perception than subadults

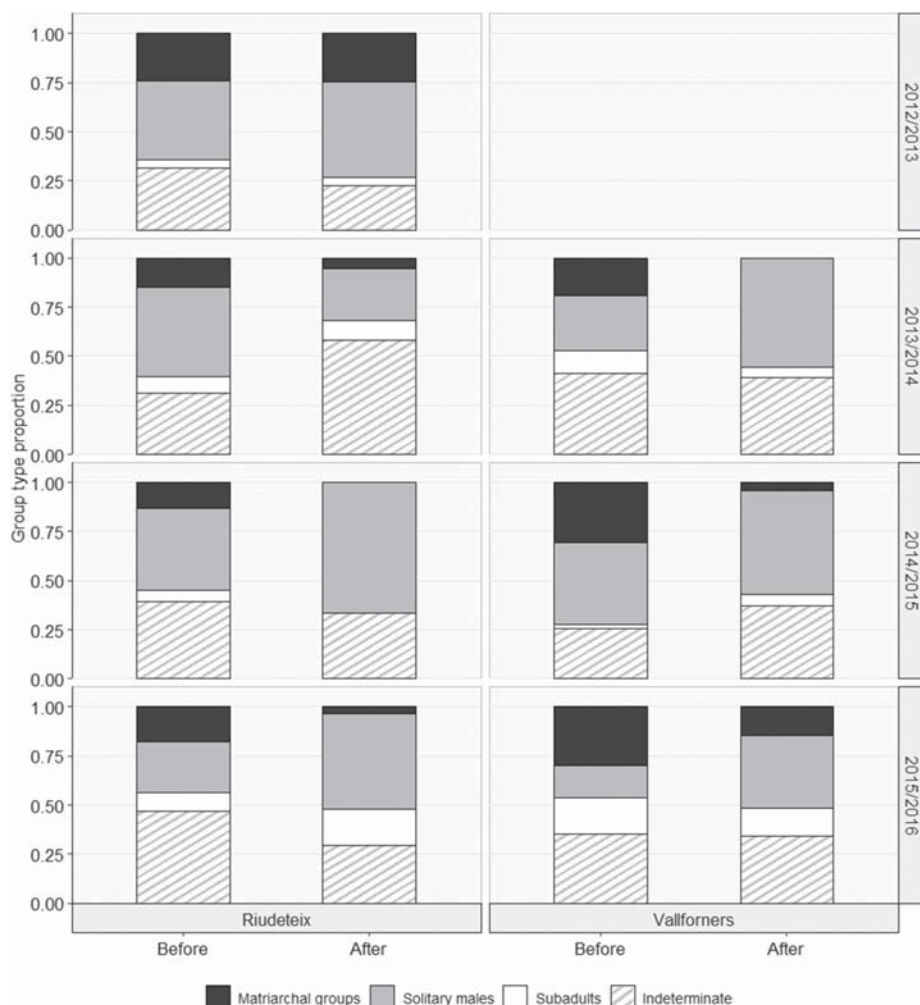


Fig. 6. Group composition proportions observed in the two study sites before and after the population control hunts inside the reserves.

and solitary males, as suggested by Saïd et al. (2012). Iacolina et al. (2009) reported that high hunting pressure may lead to an increase of aggregations of unrelated adult females suggesting that hunting may increase contact rates between otherwise different matriarchal groups. Wild boar group disruption, especially if the leading sow and other adult females are culled can also cause an increase of the juvenile dispersion (Moennig et al., 1999), once again leading to a potential increase in contact rate, which represents a major risk of disease transmission (Podgórski et al., 2018).

Little attention has been paid so far to the effect of hunting on wild boar social disruption, although the latter could have significant effects on disease control, particularly for those diseases that are contact-rate or density dependent. For instance, culling-induced social perturbation, reported in European badgers (*Meles meles*), led to increased contacts between neighbouring social groups and was in turn associated to a rise of bovine tuberculosis prevalence (Riordan et al., 2011). Similar results were reported for alpine ibex (*Capra ibex*) as home range perturbations due to culling led to a brucellosis re-emergence (ANSES, 2015).

These findings have major implications for mitigating human-wild boar conflicts. In contexts where wild boar high densities are associated with negative impacts, such as crop damage, reduction of biodiversity,

and vehicle collisions, reserves may act as sinks when hunting occurs in the surrounding grounds but also as sources of wild boar once the hunting season is over. This study suggests that single population control driven hunts carried out in non-hunted areas may achieve a significant reduction of individual numbers. Thus, banning hunting in some areas during a part of the hunting season will concentrate wild boar which will later allow to increase the effectiveness of methods such as culling or trapping.

These results are also relevant to manage disease outbreaks. For instance, current recommendations to control ASF include establishing a core area around the outbreak, surrounded by a buffer zone, which is in turn surrounded by an outer zone. Soon after the outbreak declaration, hunting is banned in the core and buffer zones and allowed only in the outer zone. After a certain time, the core and buffer areas are to be depopulated through intensive culling (Jori et al., 2020). Recent studies based on modelling of wild boar contact rates in North America, suggest that a 2 km culling radius around the disease detection might be sufficient to stop the spread, nevertheless, it would vary depending on the density and home range of the infected populations (Yang et al., 2021). The method used for culling should be chosen as the most efficient, causing the least possible disturbance and taking into account the local habitat and hunting traditions (Jori et al., 2020). In the study area driven hunt is

by far the most used hunting method while other methods such as lying-in wait or stalking are barely practiced. The findings of this study confirm that regular driven hunts are an effective method of concentrating wild boar in relatively small areas where animals can then be removed by culling. Nevertheless, as highlighted by a recent study in South Korea, the human intervention in ASF infected areas represents an important risk of disease spread, particularly if biosecurity measures are not properly adopted, and trapping methods can be the most effective intervention in some situations (Jo and Gortázar, 2021).

The results of several studies suggest that driven hunts can increase the wild boar movements over wider areas (Maillard et al., 1996; Sodeikat and Pohlmeier, 2003) and cause group disruptions, as we found in the present study, potentially leading to an intensification of contacts with other wild boar groups and to an increased risk of disease transmission. Yang et al. (2021) did not detect any effect of culling on contact rates in low removal situations but suggest that higher culling pressure could lead to an increase of contact rate and disease spread.

The 'reserve effect' and the fact that wild boar densities temporary increase in non-hunted areas could also be exploited to maximise the impact of vaccination campaigns based on baits containing drugs such as classical swine fever vaccines. Future studies should explore this idea and assess whether a temporary, hunting-induced increase in concentration of wild boar can be used to increase bait uptake.

4.1. Conclusions

This study corroborated the 'reserve effect' as wild boar use non-hunted areas as a refuge when hunting occurs in the surroundings. The results also demonstrate that exceptional population control driven hunts undertaken inside these areas, are an effective method in reducing number of individuals, but may also cause a disruption of wild boar social groups, potentially increasing contact rates between groups. These findings indicate that detecting or creating these refuge areas could be used to improve the efficiency of population control and to mitigate the conflicts caused by this species. The results also support the creation of different types of areas around outbreaks of diseases such as ASF, where culling is either banned or encouraged according to the need to reduce disease transmission and minimise wild boar movements between areas.

CRedit authorship contribution statement

Joana Colomer: Data curation, Formal analysis, Writing – original draft. **Carme Rosell:** Conceptualization, Methodology, Resources, Writing – review & editing. **José Domingo Rodríguez-Teijeiro:** Supervision, Methodology, Writing – review & editing. **Giovanna Massei:** Supervision, Conceptualization, Writing – review & editing.

Declaration of competing interest

No conflict of interest exists.

Acknowledgements

This research was supported by the Montseny natural park and the 'Pla de Doctorats industrials' of the Catalan Government. We thank our colleagues from Minuartia and the Montseny natural park rangers who carried out the field work and the support of the 'Evolutionary ecology, behaviour and biodiversity conservation' research group.

We would like to specially thank our colleagues Daniel Guinart, from Montseny natural park, and Ferran Navàs from Minuartia who provided valuable contributions that greatly assisted the research.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2021.148721>.

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