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WILD BOAR MOVEMENT ECOLOGY ACROSS SCALES

Insights from a population expanding into agroecosystems of Southern Belgium

Kevin MORELLE

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Promoteur : Prof. Philippe LEJEUNE

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SUMMARY

Over the time, ungulates have seen their populations continuously changing under the effect of direct, i.e. hunting pressure, and indirect, i.e. land-use changes, human activities. Under control until recently, ungulates have progressively adapted to these modifications and are now able to cope with human-shaped environments, consequently their number and range have greatly and worryingly increased. More particularly, among ungulates species, the wild boar *Sus scrofa* raises important concerns due to its environmental, economic and social impacts on modern societies. Understanding the ecology of ungulates species and their ability to survive within highly dynamic and seasonal ecosystems, such as agricultural environment, is thus necessary to better mitigate their negative impacts and to sustainably manage growing and expanding populations.

Although only recently studied, movement ecology of animal is an important species trait that allows animal to adapt to rapid environmental changes. Considering movement as the resulting interaction of the animal's internal state, navigation and motion capacity as well as of the effect of the surrounding environment ("external factors"), provides a clear conceptual framework enabling to study patterns, mechanisms and processes, such as coping with land-use changes.

In this thesis, we study the case of an expanding wild boar population in Southern Belgium and consider the movement ecology of the species to understand how wild boar colonize and flourish in agroecosystems. More specifically, the thesis aims at i) reviewing quantitatively and qualitatively the scientific literature about wild boar movement ecology, and ii) analyzing the spatial response of wild boar to agroecosystems in terms of movement and habitat selection across three spatial and temporal scales.

The literature review highlights that wild boar is the least studied ungulates species in terms of movement ecology. We suggest that this is likely due i) to the relative complexity of fitting tracking devices to this species, and ii) to its generalist diet making the species not suitable to test foraging hypotheses. Among existing studies, a large part focuses on the role of external factors (e.g. hunting, landscape features) on movement while others components of the movement

ecology framework (internal state, navigation and motion capacity) remain poorly studied. However, when assuming behavioral similarity between wild and domestic boars, experimental studies on captive animals show how wild boar can develop complex movement strategies by using their highly developed cognitive and sensory abilities, and spatial memory.

The spatio-temporal analysis suggests a scale-specific response of wild boar to agricultural habitat. At the intermediate scale (landscape, seasonal), wild boar uses seasonal habitat shift strategies towards agricultural areas, while at broader scale (regional, decades), wild boar avoids this habitat, preferring the forest habitat to spread and extend its occupancy range. This results in a contradiction with our preliminary hypothesis that increased area of cultivations providing cover (maize, rapeseed, cereals) facilitates wild boar population expansion. Furthermore, we show that besides the use of forest habitat, high population density is a major driving factor of the colonization of agroecosystems by wild boar. The fine-scale analysis (home range, daily), highlights the large variety of spatial behaviors (area restricted search, central place foraging, nomadism, dispersing) wild boar is able to use to cope with heterogeneous environments.

In terms of management of the species, the results of this thesis suggest that it is required to lower the population density in order to limit the population spread into agroecosystems, not only at the margin of expansion but all over the species' range. Furthermore, we recommend developing more flexible control strategies taking into account both the spatial abilities of the species and the complexity and dynamics of the environment. For example, the creation of a seasonal landscape of fear could be promoted, i.e. reducing attractivity of agricultural lands by increasing risk sensation (e.g. hunting with dogs all along the growing season). However, in our opinion, the success of any management strategy requires first to tackle the issue of the decreasing number of hunters observed in large part of Europe and to improve communication among the different stakeholders (hunting associations, farmers, public administration). Indeed, while ungulates have progressively adapted to human-induced changes, the capacity of humans to adapt to this new human-ungulate relation is questionable.

RÉSUMÉ

Au cours du temps, les ongulés sauvages ont vu leurs populations constamment évoluer sous l'effet direct de la pression de chasse et, indirecte des changements d'occupation du sol liés aux activités humaines. Encore sous contrôle récemment, les populations d'ongulés se sont progressivement adaptées aux milieux anthropisés, avec comme conséquence une augmentation inquiétante de leur nombre et de leur aire de distribution au cours des dernières décennies. Le sanglier *Sus scrofa*, en raison de son impact environnemental et socio-économique négatif, est l'ongulé sauvage soulevant actuellement les plus grandes préoccupations. Comprendre l'écologie de cette espèce et sa capacité d'adaptation aux agroécosystèmes, est nécessaire afin de permettre une meilleure gestion de l'espèce dans ces milieux.

Un moyen aisé pour les espèces mobiles de s'adapter aux changements de conditions environnementales, est leur capacité de déplacement. L' « écologie des mouvements », récent domaine de recherche en écologie animal, décrit le déplacement d'un animal comme la résultante de l'interaction entre son état interne, sa capacité de navigation, sa capacité de locomotion et des facteurs externes (p.ex. prédateurs, ressources, conspécifiques, barrières naturelles ou anthropiques). Ce cadre conceptuel clair et simple permet d'étudier les mécanismes et les processus influençant le comportement spatiale de toute espèce mobile.

Dans cette thèse, je considère comme modèle biologique l'expansion d'une population de sangliers dans le sud de la Belgique et fait l'hypothèse que l'écologie des mouvements de cette espèce est l'un des facteurs principaux expliquant son adaptation aux agroécosystèmes. Pour tester cette hypothèse, j'ai i) examiné quantitativement et qualitativement la littérature scientifique portant sur l'écologie des mouvements, ii) analysé la réponse du sanglier aux agroécosystèmes à trois échelles spatiales et temporelles, en termes de mouvement et de sélection de l'habitat.

Les résultats de la revue de la littérature montrent que le sanglier est l'ongulé sauvage le moins étudié en terme d'écologie des mouvements. Les raisons avancées relèvent de i) l'inadéquation des dispositifs de marquage et suivi à la morphologie de l'espèce (absence

de cou) et ii) son alimentation généraliste faisant du sanglier un candidat non idéal pour tester des hypothèses et théories. Parmi les études existantes, un grand nombre porte sur le rôle des facteurs externes (par ex. chasse, structure du paysage) alors que les autres composantes (état interne, capacité de navigation et capacité de locomotion) demeurent peu étudiées. Cependant, en prenant en compte les études expérimentales réalisées sur des animaux en captivité, nous avons pu mieux comprendre comment le sanglier peut mettre en place des stratégies de mouvement complexes grâce à leur faculté cognitive, sensorielle et de mémoire spatiale très développée.

L'analyse spatio-temporelle suggère une réponse échelle-dépendante du sanglier à l'habitat agricole. À l'échelle intermédiaire (paysage, saison), le sanglier utilise cet habitat de façon saisonnière, alors qu'à plus large échelle (régionale, décennies), le sanglier évite cet habitat, lui préférant l'habitat forestier pour coloniser des zones inoccupées. Ce résultat est en contradiction avec l'hypothèse de départ posée que l'augmentation des cultures offrant un couvert et/ou de la ressource alimentaire (p.ex. maïs, colza, céréales, miscanthus) facilite l'expansion de la population de sangliers. L'analyse démontre également que l'augmentation des densités est un facteur contributif majeur de la colonisation des agroécosystèmes par les sangliers. L'analyse à fine échelle (locale, journalier), souligne la grande variété de comportements spatiaux (zones de recherche restreintes, mouvements circulaires, nomadisme, dispersion) dont sont capables les sangliers en milieu hétérogène.

En termes de gestion de l'espèce, les résultats de cette thèse suggèrent que limiter la propagation de l'espèce dans les agroécosystèmes, nécessite de réduire la densité de la population non seulement dans sa zone d'expansion, mais également dans toute l'aire occupée par l'espèce. En outre, nous recommandons de développer des stratégies de contrôle prenant en compte à la fois les capacités spatiales de l'espèce et la complexité des agroécosystèmes. Par exemple, la création saisonnière d'un « paysage de la peur », pourrait permettre de réduire l'attractivité des terres agricoles en augmentant la sensation de risque (par ex. chasse accompagnée de chiens durant la période de culture). Cependant, le succès de toute stratégie de gestion nécessitera en premier lieu de s'attaquer à la question de la diminution du nombre de chasseurs observée en Europe et d'améliorer la communication entre les différentes parties prenantes (associations de chasseurs, agriculteurs, administration publique). En effet, alors que les ongulés se sont progressivement adaptés aux changements induits à l'environnement par l'homme, (re)trouver un équilibre entre les hommes et les grands ongulés, repose en grande partie sur la capacité des humains à s'adapter à cette nouvelle donne et proposer des mesures adaptées.

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PUBLICATIONS

PAPER I

Morelle K, Lehaire F, Lejeune P 2014. Is Wild Boar Heading Towards Movement Ecology? A Review of Trends and Gaps. *Wildlife Biology* 20(4):196-205. handle: 2268/ 171942

PAPER II

Morelle K, Podgórski T, Prévot C, Keuling O, Lehaire F, Lejeune P 2015. Towards understanding wild boar Sus scrofa movement: a synthetic movement ecology approach. *Mammal Review* 45(1):15-29. handle: 2268/ 172317

PAPER III

Morelle K, Bunnefeld N, Oswald SA, Lejeune P From GPS tracks to fine-scale, behavioural movement strategies: a straightforward approach for identifying multiple spatial behaviours. *Manuscript*

PAPER IV

Morelle K, Lejeune P 2014. Seasonal variations of wild boar Sus scrofa distribution in agricultural landscapes: a species distribution modelling approach. *European Journal of Wildlife Research* : 61(1): 45-56. handle: 2268/ 173269

PAPER V

Morelle K, Fattebert J, Mengal C, Lejeune P Invasive in its native range: wild boar range expansion in European agro-landscapes. *Manuscript*

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RESEARCH CONTEXT

Between humans and wild animal species they eat, there is a long history of interactions, where abundance and distribution of animals is continuously changing under the activities and willingness of humans (Putman et al., 2011). At first, when humans were hunter-gatherers (-1.8 million to 12 000 years ago) (Marlowe, 2005) hunting animals was for feeding purposes only. With the development of agriculture and the farmer-producer human societies during the Neolithic period, the relation with hunted animals has been modified profoundly. These societies relied increasingly on domestic species for their subsistence. Hunting activity kept its importance, though it progressively turned into management of animal populations. During the middle age (5th to 15th century) manorial societies emerged and nobles developed hunting activities for recreational purposes. The concept of "game animal" arose. This concept illustrates well the willingness of human to control the nature which for example led to the voluntary extermination of Europeans' big carnivores (wolves, lynx, bears) (Breitenmoser, 1998). Since then, game population size and distribution largely depend on human's willingness to increase or lower them (Kareiva et al., 2007). Over time, the relation between human and game species has thus became ambivalent. Ungulates taxa provides a good illustration of this complex relation, being simultaneously considered as 'wild' but also as 'part of culture' by humans (Sykes and Putman, 2014).

Wild or culturally related to humans, recent increases in density and range of some forest-dwelling ungulates (Apollonio and Andersen, 2010), e.g. wild boar *Sus scrofa*, roe deer *Capreolus capreolus* and red deer *Cervus elaphus*, suggest that these species are no more under human control or, at least, question the capacity of human to effectively manage ungulates populations. How did we get there? Does a threshold in the human-ungulate relation has been crossed? Recent studies suggest that decreasing number of hunters (Milner et al., 2006; Massei et al., 2014) and, so far, relatively poor contribution of recolonizing natural predators (Chapron et al., 2014) prevent to maintain populations at desired levels. Human-induced land-use modifications (Sala et al., 2000) also provide animals with new suitable habitats (e.g. due to land abandonment, afforestation, greener urban areas) (Acevedo et al., 2011) and larger food resources (e.g. from cultivations) from which they can benefit (Putman et al., 2011).

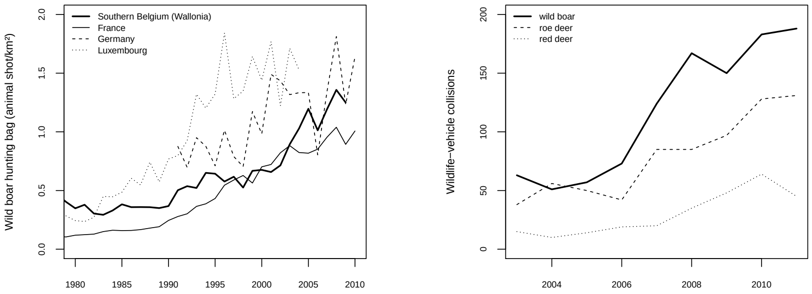
Among habitats offering suitable alternatives to forest-dwelling ungulates are agricultural lands. These agricultural lands originate from progressive reduction of the forest cover over the last centuries (Fyfe et al., 2015). Dominated by closed canopy forests until the Middle age, lowland European forests have been progressively clear-cut and opened (Birks). During this period, woodland areas and its related fauna have been excessively reduced, also in reason of the use of forest by domestic animals outcompeting wild ungulates. Since then, the continuous growth of human population has strengthened the need for arable lands (Kaplan and Zimmermann, 2009), so that agroecosystems account nowadays for more than 40% of European land area (Estreguil et al., 2012). Over the last decades, agricultural landscapes have also undergone important modifications. Under the actions of new European policies, some crops have been favored, e.g. maize *Zea mays* cultivations for livestock silage, rapeseed *Brassica napus* at the expand of wheat (Rondanini et al., 2012) and, more recently, the development of energy crops (Baka and Roland-Holst, 2009). While one could have thought that continuous opening of European landscapes would be detrimental for forest-dwelling ungulates, recent observations demonstrate the ability of species from this taxa to cope with human-shaped agricultural environments (Hewison et al., 2001; Schley and Roper, 2003; Szemethy et al., 2003).

Agricultural landscapes are highly dynamic ecosystems, in which quality of the resources and cover provided continuously change due to the seasonal cycle of farming activities. To cope with these seasonal habitat modifications, animals have to develop strategies (Smith et al., 2014). Among possible strategies, two are commonly used by animals, either by making use of their movement ability, e.g. to reach more suitable areas (Mysterud, 1999), or modifying their physiology, e.g. hibernating mammals during winter (Carey et al., 2003). Although ungulates can use both strategies to cope with seasonality, e.g body mass response of moose *Alces alces* to temperature (van Beest and Milner, 2013), their ability to migrate over long distances (Singh et al., 2012) is the most prominent and the most impacting strategy for human activities. Particularly, in dynamic environment, movement plays a key role by offering animals the ability to quickly respond to any changes in habitat composition or configuration.

It has been shown that the homogenization of European rural landscape (Jongman, 2002) potentially favors species with a large ecological spectrum and an ability to coexist with humans (McKinney and Lockwood, 1999). One such species is the roe deer which demonstrates high ability to flourish within agroecosystems, so that different species ecotypes, forested and agricultural, can be distinguished within roe deer (Hewison et al., 2001). Wild boar is also seemingly able to adapt to agroecosystems (Keuling et al., 2009), can we however speak about an 'agricultural ecotype' as for roe deer? It is one of the expected outcome of this thesis to test and observe how wild boar adapt to agroecosystems at various spatial scales.

During the last decades, populations of wild boar have increased significantly not only all over its native Eurasian range (Saez-Royuela and Telleria, 1986; Massei et al., 2014) but also where the species has been introduced by European explorers (Barrios-Garcia and Ballari, 2012). The phenomenon is thus global and causes numerous conflicts with humans: management of peri-urban populations (Cahill et al., 2012; Licoppe et al., 2014), risk of diseases transmission to livestock (Barrios-Garcia and Ballari, 2012), damages to agricultural (Herrero et al., 2006; Schley et al., 2008) and natural areas (Tolon et al., 2009).

In Southern Belgium (Wallonia), the picture is relatively similar as the one described above: continuous increase in the annual number of shot wild boars (Figure 1.1) and growing number of conflicts with humans, e.g. increase of damages caused to crops and multiplication of wild boar-vehicle collisions (Morelle et al., 2013). Furthermore, over the last three decades, the population of wild boar has expanded, invading progressively all agro-forested areas of Southern Belgium (Prévot and Morelle, 2012). This spread of the species strengthens the human-wild boar conflicts and raises the debate about the place of the species in agricultural landscapes. While cultivations dedicated to energy and fodder production have been shown to negatively affect some farmland species (Gevers et al., 2011), wild boar demonstrates a certain ability to make a profitable use of such agroecosystem environment. Structurally, the development of high cultivation, e.g. maize and rapeseed, provides shelter for the species (Keuling et al., 2009), while nutritionally, the energy-rich food seasonally available in agricultural land (Schley and Roper, 2003) favours individual growth, e.g. enhancing female fertility (Rosell et al., 2012), and consequently population growth (Geisser and Reyer, 2005).



(a) Hunting bags in Southern Belgium and different neighbouring countries

(b) Wildlife-vehicle collisions in Southern Belgium

Figure 1.1: Evolution of the hunting bags in Southern Belgium and neighbouring countries (a) and the number of wildlife-vehicle collisions between 2003 and 2011 in Southern Belgium (b).

The increased presence of wild boar in regions where agricultural activities dominate questions the current knowledge of the species' ecology and of its ability to adapt with highly dynamic ecosystem. Spatial plasticity of the species is likely to play a key role but the majority of studies has so far focused on diet and life-history traits of the species. Therefore, wild boar movement ecology and its role in the increasing presence of the species in human-dominated landscapes yet remain to be studied.

2

THESIS OBJECTIVES

Studying the presence of wild boar within agroecosystems of Southern Belgium requires thorough understanding of the processes and mechanisms that have contributed to its arrival and establishment. This thesis aims at explaining how spatial behavior of the primarily forest-dwelling wild boar has enabled the species to progressively occupy and adapt to agroecosystems, consisting of a mixture of forest and agricultural patches.

Considering the increasing body of evidences that animal habitat selection is a scale dependent process (Boyce, 2006; DeCesare et al., 2012) and that cross-scale analysis helps identifying limiting factors of habitat selection (Senft et al., 1987), we have opted for a multi-scale research design (Figure 2.1). Specifically, to understand processes and mechanisms triggering the cross-scale response of wild boar to agroecosystems, the thesis poses the following questions:

- At large scale (regional, decades): What are the mechanisms influencing the process of wild boar population range expansion from forests to agroecosystems?

- At intermediate scale (landscape, seasonal): How wild boar seasonally adapts its distribution in agroecosystems environment and what are the driving factors?

- At the local scale (local, daily): Which spatial strategies are used by wild boar to cope with agroecosystems?

Over the spatial and temporal dimension, we added a third dimension relating to the scale at which we have studied the species (population, sub-population and individuals) (Figure 2.1). This third dimension is determined by the methods used (GPS, presence indices, hunting/-damage data) in the different thesis papers and manuscripts.

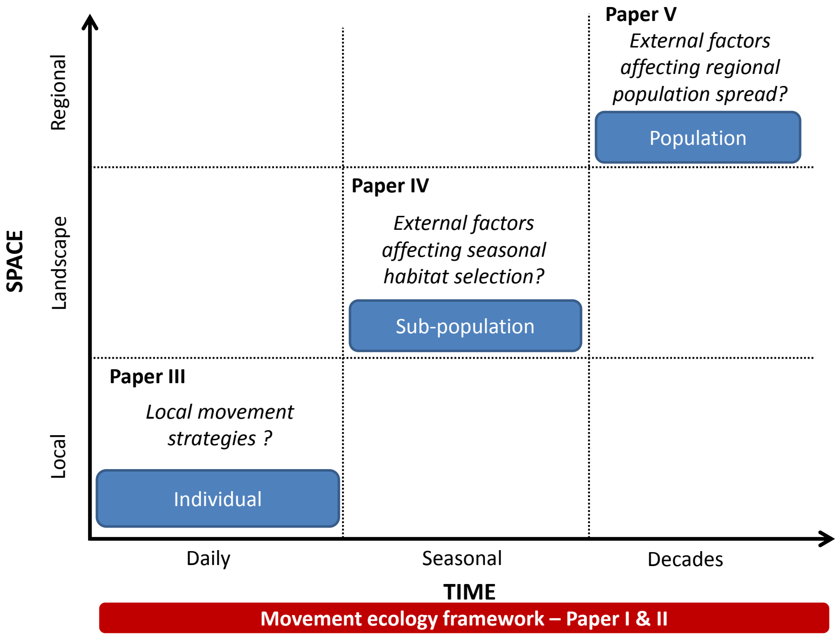


Figure 2.1: Flow chart of the research design.

Spatial ecology of animals refers to numerous theories and methods that can be used to address these questions. Specifically, our hypotheses and predictions (Table 2.1) were built up from theories borrowed to movement ecology paradigm (Nathan et al., 2008), habitat selection (Johnson, 1980), species distribution (Franklin and Miller, 2009), and population dispersal (Turchin, 1998).

Table 2.1: Main hypotheses and predictions of the thesis.

Scales	Hypotheses	Theoritical framework
Regional	Agricultural lands provide a suitable cover for wild boar population to expand. This cover allows wild boar to overcome decreasing forest cover when expanding in agroecosystems	Population dispersal
	High population density favors spread into unoccupied areas	Density-dependence
Landscape	Wild boar uses agricultural lands when it provides cover and/or food resources. However this use is inversely proportional to the distance to forest patches	Habitat selection, Spill-over, Landscape complementation/-supplementation
Local	Heterogeneous environment requires wild boar to develop multiple movement strategies	Movement ecology paradigm

3

MATERIAL AND METHODS

3.1 STUDY AREA

The study area is located in Southern Belgium (Wallonia), southerly bordered by Ardenne natural areas and northerly by the administrative linguistic border between Flanders and Wallonia (Figure 3.1). The area is characterized by a Southeast-Northwest forest gradient (80 to less than 25 % of forest cover from Ardenne to loamy regions) offering an interesting model to study the interactions between wild boar, forest and open agricultural lands. The study area is a mosaic of woods and farmlands, these latters consisting of grasslands and crops (maize, cereals, beetroot and rapeseed) while forest is patchily distributed and patch size ranges between 1 and 300 ha. The study area lies at an altitude of 50 to 350 m above sea level. Climate is sub–oceanic with a mean annual temperature of 8°C and a mean monthly temperature varying between 2 to 16°C. The mean annual rainfall is 900 mm, and the mean annual duration of snow cover is over 25 days.

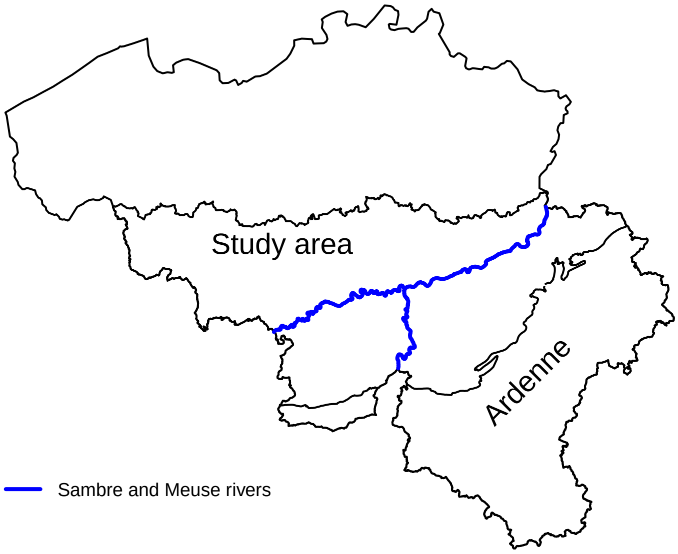


Figure 3.1: Study area localisation.

Over the last three decades, following changes in European agricultural policies, Belgian agroecosystems have rapidly evolved towards increased surface dedicated to the cultivations of maize and rapeseed offering more and more sheltering and feeding opportunities for the wild boar Figure 3.2. Also, the surface with cultivations of potato *Solanum tuberosum*, largely appreciated by the wild boar has also importantly increased between 1980 and 2008 Figure 3.2.

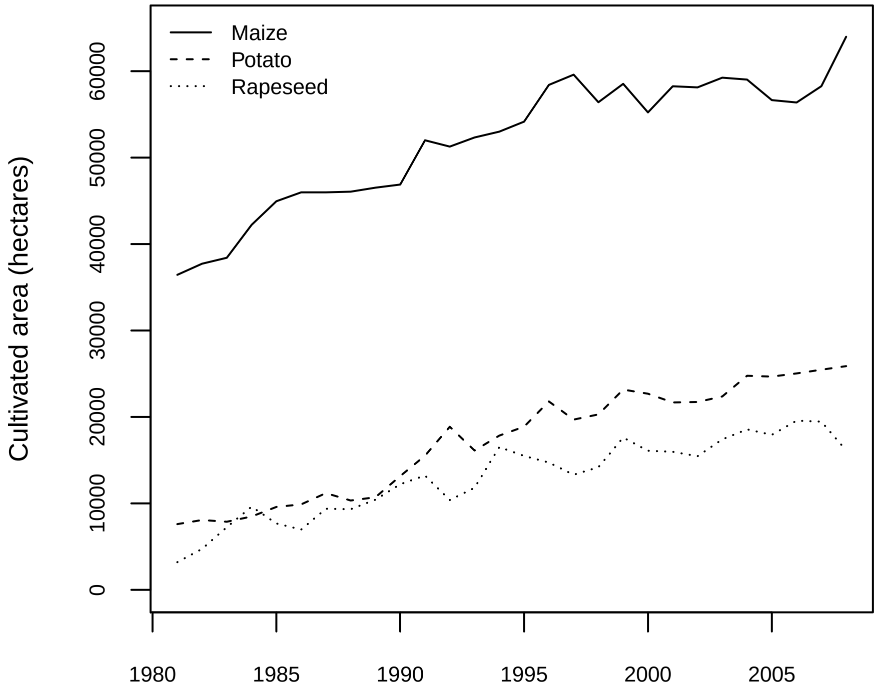


Figure 3.2: Evolution between 1980 and 2008 in Southern Belgium of some important cultivations potentially favoring the wild boar (in terms of resources and cover).

Box 1. A brief history of wild boar in Southern Belgium

Discovery of wild boar bone remains in the North Sea attests the historical presence of the species over the entire territory of Belgium until the Middle age (Toussaint and Pirson, 2011). Between AD 1500 and AD 1850, forest clearance for the development of agriculture (Delhaise and Devillez, 1991; Tallier, 2004b) together with population increase and hunting pressure restricted the range of many forest-dwelling species in Europe (Kaplan and Zimmermann, 2009). Consequently, the wild boar disappeared from many parts of its native range (Danilov and Panchenko, 2012) and, in Belgium, its distribution decreased from the North up to the highland Ardenne forest (Tallier, 2004a). Starting mid-19th century, hunting activities progressively gained in attractivity due to its economic interest. At this time, financial incomes generated by hunting were largely superior to those from forest management, so that acquisition of forests aimed at constituting a “hunting capital” rather than a “timber capital”. Between 1870 and 1940, the cost of hunting areas increased in average by 25-fold (Tallier, 2004a). As a result, game species were artificially multiplied by re-introduction (Tallier, 2004a). The upward trends slowed down during the second world-war and until the 1980's, though wild boar population size continued increasing, it remained restricted to the Ardenne forest areas. Since then the population started to expand progressively Northwards and invaded more and more agroecosystems. Despite population increase, wild boar lost his status of pest species ('bête fauve') in 1985 (Libois, 1993).

3.2 THEORETICAL FRAMEWORK

3.2.1 *Movement ecology paradigm (paper I-II-III)*

Movement is the positional change of individuals or population across spatial and temporal scales (Hansson and Akesson, 2014). Because it allows feeding, mating or escaping behaviors, moving is fundamental for all living organisms. Animal mobility is a relative concept, largely influenced by the scale of heterogeneity that an animal can perceive (Hansson and Akesson, 2014) (Figure 3.3), varying from few hundreds of meters, e.g. the home range of the Salamander *Salamandra salamandra* (Denoël, 1996), to several thousand kilometers, e.g. the seasonal migration of the Artic terns *Sterna paradise* (Egevang et al., 2010).

The movement path followed by an animal is the resulting interaction of four components, three related to the individual's own capacities: navigation, motion and internal state, and one related to external factors influencing the movement (e.g. conspecifics, natural and anthropogenic barriers) (Figure 3.4). To tell it differently, these four components aim at answering the why, where, when, how and under which external constraints an animal moves? This mechanistic view of animal displacement forms the basis of the movement ecology paradigm enabling the analysis of the spatial behavior of any moving organism in a common framework (Nathan et al., 2008).

Since the thesis deals with wild boar spatial behavior across scales, for movement both at the individual and population scale, the movement ecology framework constitutes a large theoretical part of this document. Specifically, the framework is used to review the scientific literature on a quantitative (Paper I) and qualitative (Paper II) basis. In the analysis of the expansion process of wild boar population (Paper V), we question the external factors and the navigation capacity (where

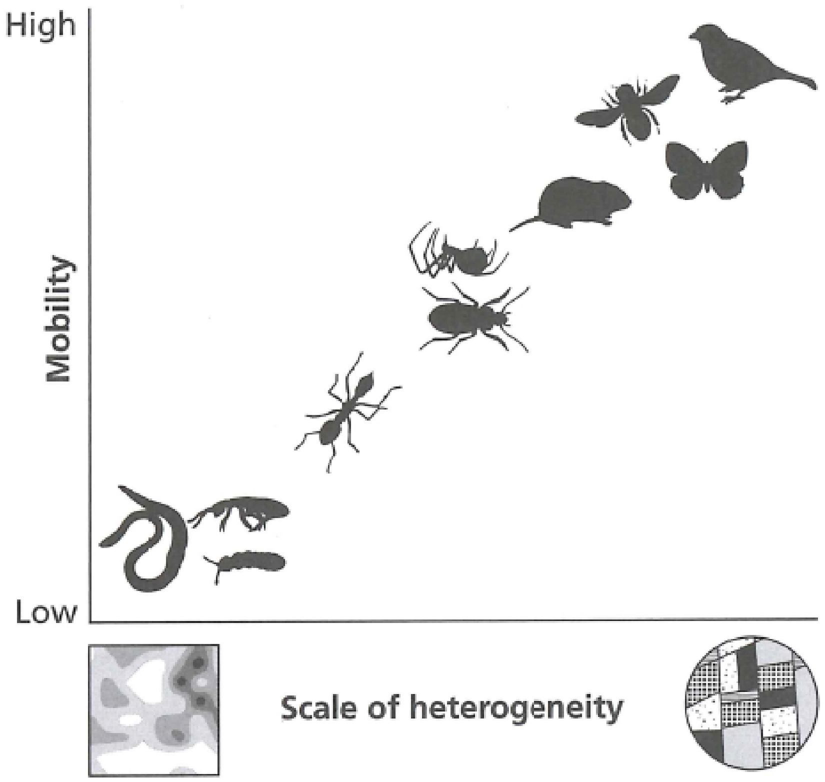


Figure 3.3: Relation between the movement ability of various taxa and their sensitivity to the heterogeneity of the environment they perceive at various scales (from local to landscape context), from Smith et al. (2014).

to move?) of the species at the regional scale. By delineating the various spatial strategies performed by wild boar at the home range scale (Paper III), we investigate the motion capacity (how to move?) of the species (Table 3.1).

3.2.2 *Habitat selection (papers IV-V)*

When animals move within or towards a habitat, they usually are in search of resources or conditions offered by this habitat. If animals were moving randomly in space, they would use these habitats proportionally to their availability (DeCesare et al., 2012). Movement path of an animal, as explained in the prior section, is a response to the surrounding environment, e.g. landscape structure (Turchin, 1991), and depends on its internal capacity, e.g. its memory (Fagan et al., 2013), its locomotor capacity (Biewener and Daniel, 2010) and its navigational capacity (Muheim et al., 2014). Therefore, movement is unlikely to be completely random and, while moving, the use

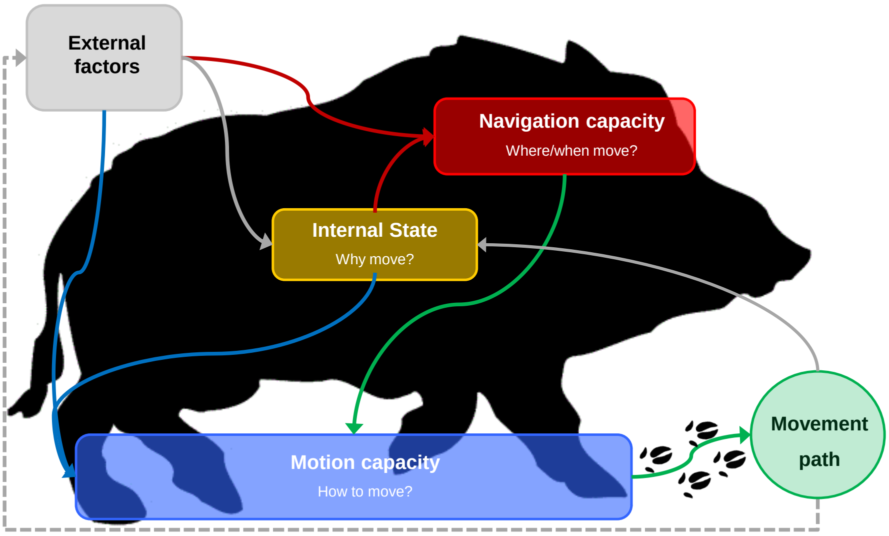


Figure 3.4: Components of the movement ecology framework. Adapted from Nathan et al. (2008).

made by animal of different habitats is rarely proportional to their availability. The observed difference between the use and the availability highlights the animal's needs for specific habitat resources or conditions, i.e. delineate the habitat preferences of the animal. The use-availability relation constitutes the basis of most of the habitat selection and species distribution models (Johnson, 1980).

Animal resource selection is a complex scale-dependent process (Johnson, 1980). Analysis of animal-habitat relation over different scales is essential to understand the habitat suitability patterns as perceived by organisms in complex landscapes and the environmental factors that influence organism–habitat relationships. Johnson proposes four scales at which behavioral response of animal can be observed, i.e. scale over which animal makes a disproportionate use ('select') of some landscape components: 1st- selection of the species' geographical range, 2nd- selection of the individual or social group home range, 3rd- selection of habitat components within the home range and 4th- selection of food items within the habitat component. In the framework of this thesis, we address three levels of selection that we also adapt by considering the specific need of our research questions (Meyer and Thuiller, 2006; DeCesare et al., 2012): 1st- selection of the habitat along the expansion process within the population range (Paper V), 2nd- selection of seasonal home range within the

Table 3.1: Components of the movement ecology framework tested within this thesis.

Movement ecology component	Scale	Research question
External factors	Seasonal	Role of environmental variables on the distribution?
	Decades	Role of environmental/population/-climatic variables on the population expansion movement – which habitat is favored?
Navigation capacity	Seasonal	Going to which habitat at which season?
	Decades	Where to spread?
Motion capacity	Daily	Which strategy to use? How to move?
Internal state	Decades	Why spreading?

sub-population range (Paper IV), 3rd- individual level of movement (and not selection) within the home range (Paper III).

Habitat selection, habitat suitability models and species distribution models take their roots in the species niche concept.The niche is considered as a property of a species defining the *environmental dimensions within which that species can survive and reproduce* (Hutchinson, 1957). This definition suggests that the distribution of a species is influenced by multiple factors, and the aim of species distribution/habitat suitability models or habitat selection analysis is to identify those factors, i.e. habitat resources or conditions required by a species. Models are indeed useful tools to understand the role of environmental factors on a species' distribution. They offer the possibility to extract from the species-niche relationship the most influential factors and to convert the relation into levels of habitat suitability (Hirzel and Le Lay, 2008). To convert niche concept into model, the use of habitat can be inferred by the occurrence of individuals of the considered species, i.e. recorded locations of animals, within that habitat (Gaillard et al., 2010).

In complex heterogeneous environments, the niche concept requires to be complemented by concepts borrowed from landscape ecology. In agroecosystems for example, resources are heterogeneously distributed in space and time so that movement of organisms between patches is necessary to access to the resources. Habitat shift, spill-over, landscape complementation and supplementation refer to process of multiple habitats use. In the case of a simplistic two habitat types landscape, e.g. made of forest and crop patches, these concepts differ in i) the spatial and temporal scale considered, and ii) the relative importance between the two habitat used. Landscape complementation occurs at the individual scale and translates the need of complementary (non-substitutable) resources available in different habitats (Dunning et al., 1992). Landscape supplementation refers to the use of additional habitat to supplement insufficient resources in prime habitat (Smith et al., 2014). We define habitat shift as the generic term encompassing any spatio-temporal change between two main habitats of an individual/population range. The concept of spillover is a process acting at the population scale and referring to the cross-boundaries movement between two habitats, following human-induced land-use changes. It is often observed in generalist species (Blitzer et al., 2012).

3.2.3 *Population expansion (paper V)*

Under the effect of environmental, e.g. climate change (Thomas et al., 2001), land-use modifications (Acevedo et al., 2011) or human introduction or translocation (Acevedo and Cassinello, 2009), the distribution and occupancy range of a species can see its margins evolving, i.e. expanding or being reduced. Here, we consider population expansion as the result of the movement of individuals located at the margin of the range towards previously unoccupied areas. Linking individuals to population movement is one of the current challenge in animal spatial ecology (Hawkes, 2009), since usually only a low sample of the whole population can be tracked (making difficult to reach a representativeness). To overcome this limitation, one can use methods enabling to track changes of population distribution over time and space, e.g. information on historical presence/absence of animal, as examplified with data used in Paper V.

3.3 METHODS IN BRIEF

Depending on the research question and the spatial and temporal scales addressed, we use different types of data. Basically, four types of data are used: scientific literature (paper I-II), GPS tracks of individuals (paper III), hunting bag and farming data (paper IV) and hunter-based knowledge (paper V). We considered that all these data can provide information on the spatial ecology of wild boar across different scales.

For more details on the methods and material used we refer the interested reader to the different Papers and manuscripts of the Appendix.

4

MAIN RESULTS AND DISCUSSION

Note: The thesis is split into five chapters, each presenting a published paper or a manuscript.

In Paper I and Paper II, we use the movement ecology paradigm (Nathan et al., 2008) as analytical framework to synthesize quantitatively and qualitatively the current knowledge from the scientific literature on wild boar movement ecology.

In the first review (**PAPER I**), we show that the study of wild boar movement ecology presents some gaps. Overall, external factors have been studied, e.g. impact of hunting or landscape features on habitat use, while animal's motivation, navigation and motion capacity remain poorly considered. By comparing wild boar with other ungulates species, we have highlighted that wild boar is currently the least studied ungulate in terms of movement ecology. Among potential reasons explaining this situation: the complexity of collar fitting and the generalist behavior of the wild boar making the species not the best candidate model for testing ecological theories, e.g. foraging hypotheses. In our opinion, to fill the gap in the movement ecology of the species, effort shall focus on the development of tracking devices adapted to the physiognomy and behavior of wild boar, e.g. miniaturization of GPS technology and batteries. Furthermore, there is a need to propose original and relevant hypotheses based on ecological theories and adapted to generalist species.

Though wild boar is the least studied ungulate species in terms of movement ecology, the scientific literature on this topic is not inexistent. With the qualitative review (**PAPER II**), we synthesized current knowledge on the navigation capacity, motion capacity, internal state and external factor's role on wild boar movement ecology. We show that among external factors studied, effect of hunting on wild boar spatial use is a central question of the species' ecology. This observation highlights the importance but also the issues related to the management of this species. The review also demonstrates how suids could easily adapt to various environmental conditions by recalling on their well-developed spatial memory, cognitive ability and sensory capacity. These observations however mostly originate from experimental studies on captive individuals (domestic, hybrid but rarely wild boar). How individuals use their cognitive abilities in the wild remains to be addressed. In Paper II, we finally suggested some recently developed methods taken from the scientific literature as potential starting point to tackle these questions.

More generally, these two reviews illustrate how movement can be directly measured or indirectly inferred by means of different approaches. There is indeed not a unique −telemetric (radio or GPS tracking)- adapted method to study animal movement, but many other methods, e.g. genetic tools, direct observations, animal indices, that can be used to infer spatial displacement of animal at different scales. The combined use of advanced tracking methods, allowing observation of fine-scale movement, together with these other indirect methods, indicating on broader scale movement, provides an effective way to study movement of animal across spatial and temporal scales, as exemplified by this thesis.

In **PAPER III**, we proposed a new framework combining validated methods to decompose the movement path of GPS-tracked individuals into short and coherent spatial behaviors. Firstly, we have used the behavioral change point analysis (Gurarie et al., 2009) to segment the whole track into hourly to daily bouts presenting similar movement parameters (turning angle and speed). Secondly, by means of the net squared displacement modeling (Bunnefeld et al., 2011), we have classified these bouts into coherent spatial strategies. Testing this approach on GPS tracks of wild boar subadults, we have been able to observe five main spatial strategies: area restricted search, dispersal, nomadism, central place foraging behavior and stationarity. This result extends prior attempt to classify daily movements of wild boar by means of visual analysis of the net displacement-time relation (Spitz and Janeau, 1990). Compared to visual analysis, this method presents the advantage of being more objective but also fully automatized. The method could be easily applied to any kind of other species for which tracking data are available. It is easy to use and it is fully implemented within R (Team, 2013), though tuning of parameters for the behavioural change point analysis (BCPA) is required and should be based on specific needs of the species of interest (Gurarie et al., 2009).

Combined with information on spatial attributes, e.g. retrieved from Geographic Information Systems (GIS), the outcomes of this analysis allow the study of interactions between the movement strategies and the environment: which strategy is used in which habitat? At which moment of the day one strategy is used over the other? Information on the energetic budget of these different strategies could be further retrieved thanks to new generation of bio-loggers (Boyd et al., 2004).

While individuals can use different movement strategies to cope with landscape heterogeneities, understanding emergence of patterns at the population scale implies to consider various mechanisms which are not the scope of this thesis but important to bear in mind. Movement is indeed the consequence of multiple mechanisms, e.g. social interactions, predations risks and resources distribution acting simultenously or not on individuals. In highly social species like wild boar, movement of individuals will firstly be influenced by the presence of conspecifics. Wild boar are indeed organize in cohesive group of individuals females and their offsprings (Dardaillon, 1988), while males usually range around these groups. Associative movement of individuals and group of individuals under the constraints of these different mechanisms finally emerges into population scale distribution and abundance (Owen-Smith, 2014). Understanding mechanisms and processes occuring at the wild boar population scale is the purpose of Paper IV and V.

In **PAPER IV**, we analyse the factors that drive the seasonal distribution of the wild boar in agroecosystems, where resources are heterogeneously distributed. By means of indirect method (i.e. use of presence indices), we compared wild boar distribution during the growing (April-September) and the (main) hunting season (October-December). Our results demonstrate the ability of wild boar to exploit spatial variability in resources. Specifically the analysis shows that i) during the growing season, suitable areas for wild boar almost double, and ii) the probability of wild boar presence in agricultural lands during the growing season is related to the distance to forest. As expected, this probability of presence was higher in close proximity to forest but, more surprisingly, also over a threshold distance of about 1 kilometer. Together, these results suggest a seasonal shift in habitat by wild boar (from forest to agricultural cultivations) and a relative seasonal independence of wild boar towards forest habitat.

Seasonal variation in distribution suggests a mass movement of individuals between forest and agricultural habitats. Yet, from the approach we used, it is not possible to assess how the seasonal shift in distribution occurs at the individual scale. Are all individuals shifters? Do they expand their home range to cover both forested and agricultural areas? The relation between the distance to forest and the probability of presence suggests that agricultural areas are used at two levels. First, in direct relation to forest area, i.e. individuals staying in the vicinity of forest, and, second, at distance higher than 1 kilometer, i.e. individuals leaving temporarily the forest to shift completely to croplands. This hypothesis is corroborated by previous findings of variation in the individual response of wild boar to agricultural areas (Keuling et al., 2009). Because individuals respond differently to resource distribution and predation risk, it is however unlikely that all individuals of a population shift to agricultural lands during the growing season as illustrated in Keuling et al. (2009).

Seasonal habitat shift when performed only by a part of a population, refers to process known as partial migration, in which only one part of the population actually migrates and the other resides (Chapman et al., 2011). Wild boar is not the only ungulate demonstrating this ability to seasonally adapt its distribution in agricultural landscape. Other cases of partial shift are known for red deer (Szemethy et al., 2003) and roe deer. What are the reasons that could explain intra-specific variation in behaviour? Seasonal environments with variable and relatively unpredictable food resource and predation risk is known to favor partial migration of ungulate species (Mysterud et al., 2011). This partial migration is largely explained by forage maturation hypothesis (Hebblewhite et al., 2008). Exported to the specific case of wild boar and agroecosystems, this hypothesis would suggest that energetic food provided by crops would solely explain wild boar use of agricultural lands. Because wild boar not only uses cultivations when they provide resources and not only uses cultivations that provided resources (e.g. use of rapeseed), we suggest that otherfactors than food attractivity might play a role. For example, as shown for red deer population, predation risk, competition avoidance and social fences are other factors that can influence habitat selection (Mysterud et al., 2011). The predation/food resource ratio can indeed greatly vary at various temporal scales and shape animal propensity to shift habitat.

In terms of landscape ecology, croplands and forests according to the time scale considered constitute complementary and supplementary habitats for wild boar. In summer, the use of both habitats relates to a landscape supplementation process, in which forest does not provide sufficient resources or is not attractive enough to retain wild boars. In consequence they use highly energetic resources from human-modified habitat, i.e. agricultural lands. However, between seasons, the use of forest and agricultural habitats constitutes an example of cross-season complementation of resources (Smith et al., 2014), where resources provided by crops allow rapid individual growth at a critical stage (piglet growth). Consequently, wild boar seasonal habitat shift can be considered as a specific case of inter-seasonal landscape complementation and intra-seasonal landscape supplementation (Dunning et al., 1992).

Moreover, our results underscore the question whether agricultural areas shall be considered as matrix or patch for the wild boar. Providing cover and food, the agricultural matrix favors movement between forest patches (Prevedello and Vieira, 2010). Yet the physical structure of a crop cultivation is different than one of a forest patch, and probably requires more sensory ability for wild boar as well as probably does not allow the species to be protected from aversive weather.

While agricultural lands has a clear seasonal attractivity for wild boar, does this habitat enhance broader scale population movement?

In **PAPER V**, we test the role of this hypothesis (i.e. increase in crops providing cover) toghether with other hypotheses (population density, climatic conditions and natural habitat) on the range expansion of wild boar in Southern Belgium. We show that spread of wild boar is promoted by high population density at the front of expansion. The result also demonstrates the relative preference of wild boar population for forest cover to spread in the landscape. This suggests that wild boar remains a relative forest-dwelling species and that to our opinion we cannot yet speak of an 'agricultural ecotype' as for the roe deer (Hewison et al., 2001). While cultivations providing cover and resources did not affect wild boar's range expansion, we suggest that it is likely that these resources have played an indirect role in the process by sustaining population growth. Moreover, population growth could have been favored also by the relative decrease in the number of hunters over the last decades (Figure 4.1), though further analyses would be required to confirm this hypothesis (Massei et al., 2014).

Box 2. Limits of hunting statistics data.
In our different analysis, we make use of the hunting statistics provided by the Administration (Département de la Chasse et la Pêche). Hunting bags are controversial data and must consequently be analysed with cautious (Imperio et al., 2010). Their reliability as index of population abundance and consequently their use to make ecological inference

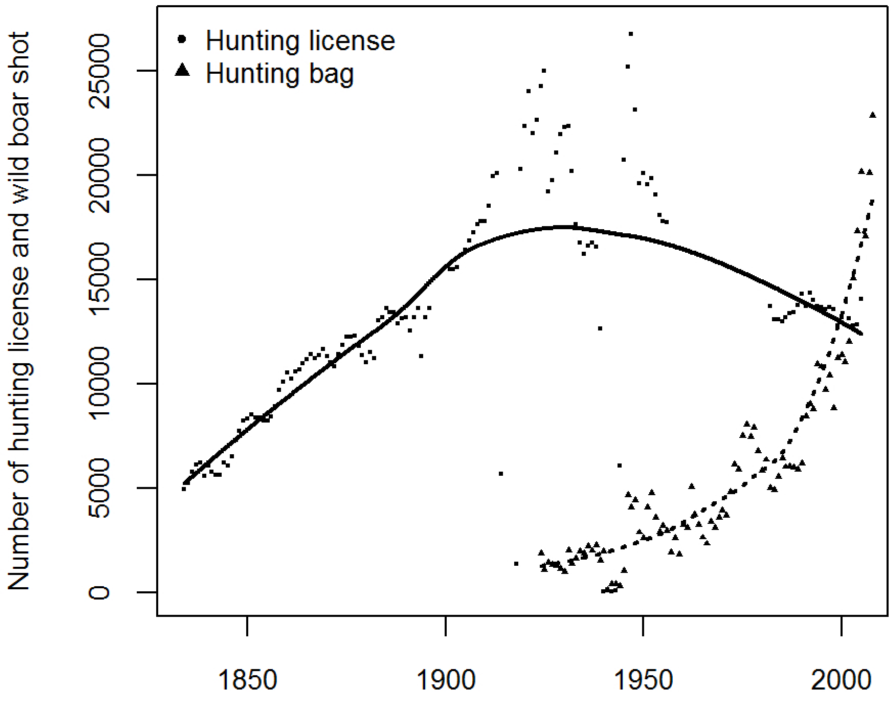


Figure 4.1: Evolution of the number of hunting licenses and the number of hunted wild boars over the two last centuries in Southern Belgium (Source: SPW-Direction de la Chasse et Pêche).

is often debated (Imperio et al., 2010). Validation via independent and correction for hunting effort are the two methods suggested to take into account bias in hunting data. In wild boar studies, hunting bags are often used as a proxy for population abundance, sometimes with correction for hunting effort, sometimes without (Bosch et al., 2012; Massei et al., 2014). We tried to retrieve hunting effort data from hunting associations (number of hunting days, and numbers of guns), but due to the lack of standardized data collection, we quickly realized using these information would increase our bias rather than reducing it (pers. obs.).

In the absence of data on hunting efforts, we tested the reliability of hunting data by comparisons with independent data sets. This test simply measure the relation between the hunting statistics and an independent measure of abundance. Here in our attempt to validate harvest indices, we used wild boar-vehicle collisions as independent data. Road accidents dataset is based on police accident statements (Morelle et al., 2013; Lehaire et al., 2013). We tested the relation with the hunting bags statistics by fitting a linear model. The results showed a significant relation (p=0.011, r-squared=0.58) with the roads collisions (Figure 4.2).

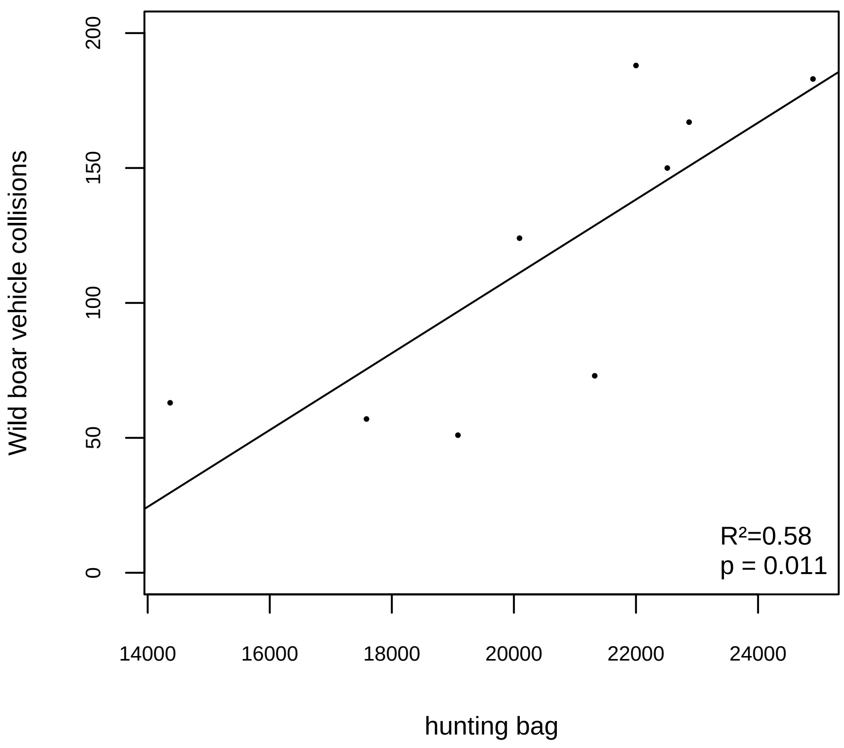


Figure 4.2: Linear relation between wild boar hunting bags and wild boar-vehicle collisions for the period 2003-2011.

This result suggests that hunting statistics in our study area are able to track trends in population changes. Does this make the use of hunting bags unquestionable for the purpose of our studies? As to concern paper III, we used data from hunting associations located in the areas recently occupied by wild boar. We used the hunting bag data not directly as a proxy of wild boar abundance but as a proxy of wild boar presence in woodland during the hunting season. While potential bias in the hunting statistics could occur and potentially provide misleading results, the method used to estimate the species distribution model, MaxENT is based on presence and pseudo absence data (Elith et al., 2011). With this method, a balanced number of presence and pseudo-absence have to be provided or generated, so that bias in the hunting statistics couldn't have affected our results. Moreover, during the period considered by this study (2009-2010), a new system of traceability was set up in Wallonia. With this new system, a bracelet is assigned to every shot wild boar. At the start of the season, hunting associations ask a defined number of bracelets, which potentially reduce the risk of bias considering that the forest administration which delivers the bracelets also control the process. As to concern paper IV, we used hunting bag statistics averaged over grid of 10 x 10 km along period of five years. By working at such a broad scale, we hypothesized that eventual bias in the data is not susceptible to affect our interpretation of the result. Though the use we made of hunting data insure a relative safety of our analysis towards bias, we took care to bring as much cautious as possible in the interpretation of our results.

5

PERSPECTIVES

The main outcome of this thesis suggests a scale-dependent trade-off towards forests habitat for wild boar living in agroecosystems, i.e. relative seasonal avoidance of forest during the growing season at the landscape scale vs. preference of forest habitat at the regional scale for population movement. This observation confirms the ability of wild boar to adapt its spatial response in dynamic ecosystems, i.e. exhibiting overall independence at local scale from forest habitat while, over large scale, the dependency on forest cover remains.

Within the framework of this thesis, the analysis of habitat selection by wild boar at different scales has been made relatively independently. A major further step that shall be achieved is the combination of the various levels of selection (local, landscape and regional) within a common nested frame allowing to integrate inferences across scale (Meyer and Thuiller, 2006; DeCesare et al., 2012). Indeed nested multi-scale analysis present the advantage of conditionally relating the different orders of selection while we arbitrarily relate them in our research design. By better integrating the different scales of analysis, we could more easily fill the gaps existing between the individual and the population level. Yet, integration of information on dispersal (Prévot and Licoppe, 2013) and on social behaviour mechanisms, e.g. fusion-fission of wild boar groups (Podgórski et al., 2014b,a), would greatly help to our understanding of what really happen between these two levels.

At the individual scale, studies on motivation of wild boar (i.e. its internal state) to shift in agricultural areas should be addressed. As highlighted by Papers I and II there is indeed a strong need for better understanding of the individual traits that favors habitat shift (who are the shifters?). The results of this thesis together with the results from other studies on wild boar (Keuling et al., 2009) or from studies on other ungulates (Szemethy et al., 2003) show a relative repeatability in the behavior of individual using the agroecosystem, suggesting potential learning process. Investigating this question is important in order to improve our understanding of how individual variability shapes population distribution (Hawkes, 2009). Additionally, moving in relatively homogeneous cropland areas (compared to forest) probably requires from the animal to recall specific navigation abilities.

The increased density of population at the margin of expansion favors the Northwards spread of the species. Though, we suggested that the decrease in the number of hunters and the increase surface of maize cultivation are likely contributing elements of the population growth, these aspects should be investigated.

Pattern of habitat use is the main driver of animal fitness performance (Gaillard et al., 2010). Relating habitat use to individual and population fitness (i.e. growth rate) remains a major ecological question to be investigated. How do individual and population respond to various spatial scales but also in various environmental conditions in terms of fitness? In this thesis, we consider a population of wild boar evolving in an agroecosystem. Fruitful comparisons with individuals and population evolving in more forested or urbanized environments would help highlighting potential phenotypic and behavioral differences. This would allow to better understand the role of agriculture use on the animal's fitness, i.e. studying more thoroughly the costs and benefits of seasonal shift in agricultural land versus residency in forest habitat. This could be done by assessing differences in the phenotypic response (weight, female fertility) of wild boar to the various environmental conditions in which the species lives. Ultimately it would provide insight on how adaptive ability of wild boar to human induced environmental change arise from intrinsic behavioral plasticity or from evolutionary adaptation (Tuomainen and Candolin, 2011).

The adaptation of common ungulates, roe deer (Hewison et al., 2001; Morellet et al., 2011), red deer (Szemethy et al., 2003) and wild boar (the present thesis) to woodland fragmentation and agroecosystems, suggests that these species have a relative high plasticity allowing them to adapt to these human-shaped environments. This adaptation of ungulates to agroecosystems requires specific management actions, not only targeting one species but potentially affecting all of them.

Preventing wild boar as well as any other ungulate species from using cropland area is probably an impossible mission. In agroecosystem, it is hardly possible to play on the seasonal distribution of the species and its use of cropland areas. However, animal habitat selection is driven by the growth/predation risk ratio (DeCesare et al., 2014).

By playing on these components it is thus possible to influence habitat selection. Acting on the 'growth' component of this relation is however relatively unfeasible. It would indeed mean modifying agricultural practices, ruled by European policies and the global market. Consequently, the only way to influence habitat selection of animal is to act on the predation risk component. Manipulating the landscape of fear in agroecosystems, e.g. increasing hunting pressure, could be used since it is an effective manner to influence animal distribution and reduce conflicting situations (Putman et al., 2011; Cromsigt et al., 2013). Rettie and Messier (2000) propose that, at broader spatial scales, animals select the factors with the most limiting fitness. Considering that for wild boar these two factors are access to food resources and to cover, selection of forest at broad scale suggests avoidance of higher predation risk in agricultural areas. However, according to our results this hypothesis is only valid at the regional scale. At the landscape and seasonal scale, predation risk within crops is seemingly not perceived high enough by wild boar to avoid these areas. To be more effective, management actions aiming at driving habitat selection should consequently insure that spatial variation of the risk reaches levels that can be perceived by animals (Hebblewhite2008).

Finally, to conclude this thesis, we propose in **Box 3** to relate the main results of this thesis to current management issues observed in Southern Belgium (Wallonia), management issues however currently encountered in most European countries (Apollonio and Andersen, 2010; Putman et al., 2011).

Box 3. Management implications

Hunting in agricultural plains

Our result have proven that wild boar not only uses agricultural areas in the vicinity of forests but also move further away and really enters the plains. Consequently, insuring hunting of wild boar over the whole agricultural plains occupied by wild boar should be promoted. We are aware that hunting in agroecosystems presents some difficulties that should be taken into account. To allow more efficient control measure, new strategies should be set up (e.g. manipulation of the 'landscape of fear', authorizing hunting at night with adapted devices, or testing unmanned aerial vehicle to detect more easily presence of wild boar in cultivated areas.

Artificial feeding

Artificial feeding can be defined as food brought by humans to wild animals. It is usually used for two purposes. Firstly dissuasive feeding which aims at preventing damage to agricultural crops. Secondly, supplemental feeding which is brought during periods where natural resources are rare or absent, usually corresponding to winter season under our latitude. Our research suggests two things: i) use of cultivations in agroecosystems is not a "one-night stand", i.e. feeding exploration back and forth from the forest. Rather, wild boar use this habitat not only for its resource quality but seemingly for its sheltering abilities; ii) high wild boar density results in spatial expansion of the population. Consequently, factors contributing to sustain or increase population densities should be avoided. Considering the unintended consequence of artificial feeding to enhance population growth and its relative unefficiency to reduce damages (Milner et al., 2014), we do not recommend this practice.

Hunting plan

Currently in Belgium, only the red deer is managed by means of a hunting plan, annually set up by the administration. Effective population control of wild boar to our sense would greatly require such a hunting plan. However developing an effective hunting plan requires annual assessment of the population or indices used as proxy for inferring population trends. Since accurate count of animal populations is a difficult task, more and more, management plans are based on ecological indicators able to infer balance between population size and its environment (Lehaire et al., 2014). Estimation of wild boar population densities being highly difficult (Morelle et al., 2012), we suggest that such ecological indicators could be used to annually assessed the population status and define accordingly the hunting pressure level to be achieved. Specifically, agricultural damages intensity and rooting to natural/artificial regeneration in forest could be used as indicators to measure the pressure exerted by wild boar on its environment.

Next to ecological indicators, the success of a management plan requires knowledge on hunting effort and success at the lowest possible scale, i.e. the hunting territory. Concretly, this would mean spatializing the information on the number of wild boar hunted per hunting territories as well as the timing, type of hunt, characteristics (weight, age accurately measured) of the animals hunted and the number of hunters involved. Ecological indicators toghether with accurate hunting statistics would allow to develop tools enabling reliable assessment of the relation between wild boar and its environment and orient accordingly management strategies.

In Belgium, hunting is basically organized around management units ("conseils cynégétiques") made of hunting territories ("territoires de chasse"), supervised by the Walloon Hunting and Fishing Department. Altoghether, these structures hold the means to develop a successful management plan for the wild boar in Southern Belgium. However, from personal observations made during our thesis, we suggest that better communication and power transfer ("transfert de pouvoir") are necessary to effectively implement a management plan. Mapping hunting territories within a geographic information system and clear statement of information required for any hunting events are necessary and should urgently be discussed between management units and the administration. Moreover we would like to suggest that not only wild boar population should be estimated, but also hunters' population. Trends in the number of hunters should be more carefully considered by the Administration in order to avoid future depletion of this necessary but unfortunatly often misregarded activity.

BIBLIOGRAPHY

Acevedo, P. and Cassinello, J., 2009. Human-induced range expansion of wild ungulates causes niche overlap between previously allopatric species: red deer and Iberian ibex in mountainous regions of southern Spain. *Annales Zoologici Fennici*, 46:39–50.

Acevedo, P., Farfán, M., Márquez, A., Delibes-Mateos, M., Real, R., and Vargas, J., 2011. Past, present and future of wild ungulates in relation to changes in land use. *Landscape Ecology*, 26(1):19–31. doi: 10.1007/s10980-010-9538-2.

Apollonio, M. and Andersen, R., 2010. *European Ungulates and Their Management in the 21st Century*. Cambridge University Press, Cambridge. ISBN 9780521760614. Monograph Wageningen UR Library.

Baka, J. and Roland-Holst, D., 2009. Food or fuel? What European farmers can contribute to Europe's transport energy requirements and the Doha Round. *Energy Policy*, 37(7):2505 – 2513. doi: http://dx.doi.org/10.1016/j.enpol.2008.09.050.

Barrios-Garcia, M. N. and Ballari, S. A., 2012. Impact of wild boar (Sus scrofa) in its introduced and native range: a review. *Biological Invasions*, 14(11):2283–2300.

Biewener, A. and Daniel, T., 2010. *A moving topic: control and dynamics of animal locomotion*, volume 6. doi: 10.1098/rsbl.2010.0294.

Birks, H. J. B. Mind the gap: how open were European primeval forests? *Trends in Ecology & Evolution*, 20(4):154–156. doi: 10.1016/j.tree.2005.02.001.

Blitzer, E. J., Dormann, C. F., Holzschuh, A., Klein, A.-M., Rand, T. A., and Tscharntke, T., 2012. Spillover of functionally important organisms between managed and natural habitats. *Agriculture, Ecosystems & Environment*, 146(1):34 – 43. doi: 10.1016/j.agee.2011.09.005.

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

Boyce, M. S., 2006. Scale for resource selection functions. *Diversity and Distributions*, 12(3):269–276. doi: 10.1111/j.1366-9516.2006.00243.x.

Boyd, I. L., Kato, A., and Ropert-Coudert, Y., 2004. Bio-logging science: sensing beyond the boundaries. *Memoirs of National Institute of Polar Research. Special issue*, 58:1–14.

Breitenmoser, U., 1998. Large predators in the Alps: The fall and rise of man's competitors. *Biological Conservation*, 83(3):279–289. doi: 10.1016/S0006-3207(97)00084-0.

Bunnefeld, N., Börger, L., van Moorter, B., Rolandsen, C. M., Dettki, H., Solberg, E. J., and Ericsson, G., 2011. A model-driven approach to quantify migration patterns: individual, regional and yearly differences. *Journal of Animal Ecology*, 80(2):466–476. doi: 10.1111/j.1365-2656.2010.01776.x.

Cahill, S., Llimona, F., Cabaneros, L., and Calomardo, F., 2012. Characteristics of wild boar (Sus scrofa) habituation to urban areas in the Collserola Natural Park (Barcelona) and comparison with other locations. *Animal Biodiversity and Conservation*, 35(2):221–233.

Carey, H. V., Andrews, M. T., and Martin, S. L., 2003. Mammalian Hibernation: Cellular and Molecular Responses to Depressed Metabolism and Low Temperature. *Physiological Reviews*, 83(4):1153–1181.

Chapman, B. B., Brönmark, C., Nilsson, J.-k., and Hansson, L.-A., 2011. The ecology and evolution of partial migration. *Oikos*, 120(12): 1764–1775. doi: 10.1111/j.1600-0706.2011.20131.x.

Chapron, G., Kaczensky, P., Linnell, J. D. C., von Arx, M., Huber, D., Andrén, H., López-Bao, J. V., Adamec, M., Álvares, F., Anders, O., Balčiauskas, L., Balys, V., Bedő, P., Bego, F., Blanco, J. C., Breitenmoser, U., Brøseth, H., Bufka, L., Bunikyte, R., Ciucci, P., Dutsov, A., Engleder, T., Fuxjäger, C., Groff, C., Holmala, K., Hoxha, B., Iliopoulos, Y., Ionescu, O., Jeremić, J., Jerina, K., Kluth, G., Knauer, F., Kojola, I., Kos, I., Krofel, M., Kubala, J., Kunovac, S., Kusak, J., Kutal, M., Liberg, O., Majić, A., Männil, P., Manz, R., Marboutin, E., Marucco, F., Melovski, D., Mersini, K., Mertzanis, Y., Mysłajek, R. W., Nowak, S., Odden, J., Ozolins, J., Palomero, G., Paunović, M., Persson, J., Potočnik, H., Quenette, P.-Y., Rauer, G., Reinhardt, I., Rigg, R., Ryser, A., Salvatori, V., Skrbinšek, T., Stojanov, A., Swenson, J. E., Szemethy, L., Trajçe, A., Tsingarska-Sedefcheva, E., Váňa, M., Veeroja, R., Wabakken, P., Wölfl, M., Wölfl, S., Zimmermann, F., Zlatanova, D., and Boitani, L., 2014. Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science*, 346(6216): 1517–1519. doi: 10.1126/science.1257553.

Cromsigt, J. P. G. M., Kuijper, D. P. J., Adam, M., Beschta, R. L., Churski, M., Eycott, A., Kerley, G. I. H., Mysterud, A., Schmidt, K., and West, K., 2013. Hunting for fear: innovating management of human–wildlife conflicts. *Journal of Applied Ecology*, 50(3):544–549. doi: 10.1111/1365-2664.12076.

Danilov, P. I. and Panchenko, D. V., 2012. Expansion and some ecological features of the wild boar beyond the northern boundary of its historical range in European Russia. *Russian Journal of Ecology*, 43 (1):45–51.

Dardaillon, M., 1988. Wild boar social groupings and their seasonal changes in the Camargue, southern France. *Zeitschrift für Säugetierkunde*, 53(1):22–30.

DeCesare, N. J., Hebblewhite, M., Schmiegelow, F., Hervieux, D., McDermid, G. J., Neufeld, L., Bradley, M., Whittington, J., Smith, K. G., Morgantini, L. E., Wheatley, M., and Musiani, M., 2012. Transcending scale dependence in identifying habitat with resource selection functions. *Ecological Applications*, 22(4):1068–1083. doi: 10.1890/11-1610.1.

DeCesare, N. J., Hebblewhite, M., Bradley, M., Hervieux, D., Neufeld, L., Musiani, M., and Mysterud, A., 2014. Linking habitat selection and predation risk to spatial variation in survival. *The Journal of Animal Ecology*, 83(2):343–352. doi: 10.1111/1365-2656.12144. 24099266[pmid] J Anim Ecol.

Delhaise, C. and Devillez, F., 1991. Histoire de la forêt wallonne face à l'agriculture. Des origines à nos jours. *Forêt Wallonne*, 13:2–12.

Denoël, M., 1996. Phénologie et domaine vital de la salamandre terrestre Salamandra salamandra terrestris (Amphibia, Caudata) dans un bois du Pays de Herve (Belgique). *Cahiers d'Ethologie*, 16:291–306. doi: http://hdl.handle.net/2268/3224.

Dunning, J. B., Danielson, B. J., and Pulliam, H. R., 1992. Ecological processes that affect populations in complex landscapes. *Oikos*, 65 (1):169–175.

Egevang, C., Stenhouse, I. J., Phillips, R. A., Petersen, A., Fox, J. W., and Silk, J. R. D., 2010. Tracking of Arctic terns Sterna paradisaea reveals longest animal migration. *Proceedings of the National Academy of Sciences*, 107(5):2078–2081. doi: 10.1073/pnas.0909493107.

Elith, J., Phillips, S. J., Hastie, T., Dudík, M., Chee, Y. E., and Yates, C. J., 2011. A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions*, 17(1):43–57.

Estreguil, C., Caudullo, G., de Rigo, D., and San Miguel, J., 2012. Forest Landscape in Europe: Pattern, Fragmentation and Connectivity. Report, European Commission.

Fagan, W. F., Lewis, M. A., Auger-Méthé, M., Avgar, T., Benhamou, S., Breed, G., LaDage, L., Schlägel, U. E., Tang, W.-w., Papastamatiou, Y. P., Forester, J., and Mueller, T., 2013. Spatial memory and animal movement. *Ecology Letters*, 16(10):1316–1329. doi: 10.1111/ele.12165.

Franklin, J. and Miller, J., 2009. *Mapping species distribution: Spatial inference and prediction.* Cambridge University Press.

Fyfe, R. M., Woodbridge, J., and Roberts, N., 2015. From forest to farmland: pollen-inferred land cover change across Europe using the pseudobiomization approach. *Global Change Biology*, 21(3):1197–212. doi: 10.1111/gcb.12776.

Gaillard, J.-M., Hebblewhite, M., Loison, A., Fuller, M., Powell, R., Basille, M., and Van Moorter, B., 2010. Habitat–performance relationships: finding the right metric at a given spatial scale. *Philosophical Transactions of the Royal Society of London B*, 365:2255–2265. doi: 10.1098/rstb.2010.0085.

Geisser, H. and Reyer, H.-U., 2005. The influence of food and temperature on population density of wild boar Sus scrofa in the Thurgau (Switzerland). *Journal of Zoology*, 267(1):89–96. doi: 10.1017/S095283690500734X.

Gevers, J., Hoye, T. T., Topping, C. J., Glemnitz, M., and Schroder, B., 2011. Biodiversity and the mitigation of climate change through bioenergy: impacts of increased maize cultivation on farmland wildlife. *GCB Bioenergy*, page 11. doi: 10.1111/j.1757-1707.2011.01104.x.

Gurarie, E., Andrews, R. D., and Laidre, K. L., 2009. A novel method for identifying behavioural changes in animal movement data. *Ecology Letters*, 12(5):395–408. doi: 10.1111/j.1461-0248.2009.01293.x.

Hansson, L. and Akesson, S., 2014. *Animal Movement Across Scales.* Oxford University Press, Oxford, UK.

Hawkes, C., 2009. Linking movement behaviour, dispersal and population processes: is individual variation a key? *Journal of Animal Ecology*, 78(5):894–906. doi: 10.1111/j.1365-2656.2009.01534.x.

Hebblewhite, M., Merrill, E., and McDermid, G., 2008. A multi-scale test of the forage maturation hypothesis in a partially migratory ungulate population. *Ecological Monographs*, 78(2):141–166. doi: 10.1890/06-1708.1.

Herrero, J., Garcia-Serrano, A., Couto, S., Ortuno, V. M., and Garcia-Gonzales, R., 2006. Diet of wild boar Sus scrofa L. and crop damage in an intensive agroecosystem. *European Journal of Wildlife Research*, 52:245–250.

Hewison, A., Vincent, J., Joachim, J., Angibault, J., Cargnelutti, B., and Cibien, C., 2001. The effect of woodland fragmentation and human activity on roe deer distribution in agricultural landscape. *Canadian Journal of Zoology*, 79:679–689.

Hirzel, A. H. and Le Lay, G., 2008. Habitat suitability modelling and niche theory. *Journal of Applied Ecology*, 45(5):1372–1381.

Hutchinson, G. E., 1957. Concluding Remarks. *Cold Spring Harbor Symposia on Quantitative Biology*, 22:415–427. doi: 10.1101/sqb.1957.022.01.039.

Imperio, S., Ferrante, M., Grignetti, A., Santini, G., and Focardi, S., 2010. Investigating population dynamics in ungulates: Do hunting statistics make up a good index of population abundance? *Wildlife Biology*, 16:205–214.

Johnson, D. H., 1980. The Comparison of Usage and Availability Measurements for Evaluating Resource Preference. *Ecology*, 61(1):65–71. doi: 10.2307/1937156.

Jongman, R. H. G., 2002. Homogenisation and fragmentation of the European landscape: ecological consequences and solutions. *Landscape and Urban Planning*, 58(2–4):211–221. doi: 10.1016/S0169-2046(01)00222-5.

Kaplan, K. M. K. Jed O. and Zimmermann, N., 2009. The prehistoric and preindustrial deforestation of Europe. *Quaternary Science Reviews*, 28:3016–3034.

Kareiva, P., Watts, S., McDonald, R., and Boucher, T., 2007. Domesticated Nature: Shaping Landscapes and Ecosystems for Human Welfare. *Science*, 316(5833):1866–1869. doi: 10.1126/science.1140170.

Keuling, O., Stier, N., and Roth, M., 2009. Commuting, shifting or remaining?: Different spatial utilisation patterns of wild boar Sus scrofa L. in forest and field crops during summer. *Mammalian Biology - Zeitschrift für Säugetierkunde*, 74(2):145–152. doi: 10.1016/j.mambio.2008.05.007.

Lehaire, F., Morelle, K., and Lejeune, P., 2013. Collisions entre véhicules et animaux en liberté : état des lieux à partir d'une enquête au sein de la police. *Forêt*, 122:13–21.

Lehaire, F., Ligot, G., Morelle, K., and Lejeune, P., 2014. Les indicateurs de la pression du cerf élaphe sur la végétation du sous-bois en forêt feuillue tempérée (synthèse bibliographique). *BASE*, 18:262–272.

Libois, R., 1993. Evolution de la situation des mammifères sauvages en Région Wallonne au cours de la décennie 1983-1992. *Cahiers d'Ethologie*, 13:77–92.

Licoppe, A., Prévot, C., Cahill, S., Bovy, C., Heymans, M., and Casaer, J., 2014. Enquête internationale sur le sanglier en zone péri-urbaine. *Forêt Wallonne*, 131:3–16.

Marlowe, F. W., 2005. Hunter-gatherers and human evolution. *Evolutionary Anthropology: Issues, News, and Reviews*, 14(2):54–67. doi: 10.1002/evan.20046.

Massei, G., Kindberg, J., Licoppe, A., Gačić, D., Šprem, N., Kamler, J., Baubet, E., Hohmann, U., Monaco, A., Ozolis, J., Cellina, S., Podgórski, T., Fonseca, C., Markov, N., Pokorny, B., Rosell, C., and Náhlik, A., 2014. Wild boar populations up, numbers of hunters down? A review of trends and implications for Europe. *Pest Management Science*, pages 492–500. doi: 10.1002/ps.3965.

McKinney, M. L. and Lockwood, J. L., 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in Ecology & Evolution*, 14(11):450 – 453. doi: 10.1016/S0169-5347(99)01679-1.

Meyer, C. B. and Thuiller, W., 2006. Accuracy of resource selection functions across spatial scales. *Diversity and Distributions*, 12(3): 288–297. doi: 10.1111/j.1366-9516.2006.00241.x.

Milner, J. M., Bonenfant, C., Mysterud, A., Gaillard, J. M., Csányi, S., and Stenseth, N. C., 2006. Temporal and spatial development of red deer harvesting in Europe: Biological and cultural factors. *Journal of Applied Ecology*, 43(4):721–734.

Milner, J. M., Van Beest, F. M., Schmidt, K. T., Brook, R. K., and Storaas, T., 2014. To feed or not to feed? Evidence of the intended and unintended effects of feeding wild ungulates. *The Journal of Wildlife Management*, 78(8):1322–1334. doi: 10.1002/jwmg.798.

Morelle, K., Bouché, P., Lehaire, F., Leeman, V., and Lejeune, P., 2012. Game species monitoring using road-based distance sampling in association with thermal imagers: a covariate analysis. *Animal Biodiversity and Conservation*, 35(2):253–265.

Morelle, K., Lehaire, F., and Lejeune, P., 2013. Spatio-temporal patterns of wildlife-vehicle collisions in a region with a high-density road network. *Nature Conservation*, 5(0):53–73. doi: 10.3897/nature-conservation.5.4634.

Morellet, N., Van Moorter, B., Cargnelutti, B., Angibault, J.-M., Lourtet, B., Merlet, J., Ladet, S., and Hewison, A. J. M., 2011. Landscape composition influences roe deer habitat selection at both home range and landscape scales. *Landscape Ecology*, 26(7):999–1010. doi: 10.1007/s10980-011-9624-0.

Muheim, R., Boström, J., Akesson, S., and Liedvogel, M., 2014. *Sensory mechanism of animal orientation and navigation.* Oxford University Press, Oxford, United Kingdom.

Mysterud, A., 1999. Seasonal migration pattern and home range of roe deer (Capreolus capreolus) in an altitudinal gradient in southern Norway. *Journal of Zoology*, 247(04):479–486. doi: 10.1111/j.1469-7998.1999.tb01011.x.

Mysterud, A., Loe, L. E., Zimmermann, B., Bischof, R., Veiberg, V., and Meisingset, E., 2011. Partial migration in expanding red deer populations at northern latitudes – a role for density dependence? *Oikos*, 120(12):1817–1825. doi: 10.1111/j.1600-0706.2011.19439.x.

Nathan, R., Getz, W. M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., and Smouse, P. E., 2008. A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences of the United States of America*, 105(49):19052–19059. doi: 10.1073/pnas.0800375105.

Owen-Smith, N., 2014. Spatial ecology of large herbivore populations. *Ecography*, 37(5):416–430. doi: 10.1111/j.1600-0587.2013.00613.x.

Podgórski, T., Scandura, M., and Jędrzejewska, B., 2014a. Next of kin next door – philopatry and socio-genetic population structure in wild boar. *Journal of Zoology*, 294(3):190–197. doi: 10.1111/jzo.12167.

Podgórski, T., Lusseau, D., Scandura, M., Sönnichsen, L., and Jędrzejewska, B., 2014b. Long-Lasting, Kin-Directed Female Interactions in a Spatially Structured Wild Boar Social Network. *PLoS ONE*, 9 (6):e99875. doi: 10.1371/journal.pone.0099875.

Prevedello, J. and Vieira, M., 2010. Does the type of matrix matter? A quantitative review of the evidence. *Biodiversity and Conservation*, 19(5):1205–1223. doi: 10.1007/s10531-009-9750-z.

Prévot, C. and Morelle, K., 2012. Potentiel de dispersion du sanglier et historique de la colonisation de la plaine agricoles en Wallonie. *Forê*, 121:35–42.

Prévot, C. and Licoppe, A., 2013. Comparing red deer (Cervus elaphus L.) and wild boar (Sus scrofa L.) dispersal patterns in southern Belgium. *European Journal of Wildlife Research*, 59(6):795–803. doi: 10.1007/s10344-013-0732-9.

Putman, R., Apollonio, M., and Andersen, R., 2011. *Ungulate management in Europe: Problems and practice*. Cambridge.

Rettie, W. J. and Messier, F., 2000. Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. *Ecography*, 23(4):466–478. doi: 10.1111/j.1600-0587.2000.tb00303.x.

Rondanini, D. P., Gomez, N. V., Agosti, M. B., and Miralles, D. J., 2012. Global trends of rapeseed grain yield stability and rapeseed-to-wheat yield ratio in the last four decades. *European Journal of Agronomy*, 37(1):56–65. doi: 10.1016/j.eja.2011.10.005.

Rosell, C., Navàs, F., and Romero, S., 2012. Reproduction of wild boar in a cropland and coastal wetland area: implications for management. *Animal Biodiversity and Conservation*, 35(2):209–217.

Saez-Royuela, C. and Telleria, J., 1986. The increased population of the wild boar (Sus scrofa L.) in Europe. *Mammal Review*, 16(2):97–101.

Sala, O. E., Stuart Chapin, F., III, Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L. F., Jackson, R. B., Kinzig, A., Leemans, R., Lodge, D. M., Mooney, H. A., Oesterheld, M., Poff, N. L., Sykes, M. T., Walker, B. H., Walker, M., and Wall, D. H., 2000. Global Biodiversity Scenarios for the Year 2100. *Science*, 287 (5459):1770–1774. doi: 10.1126/science.287.5459.1770.

Schley, L. and Roper, T. J., 2003. Diet of wild boar Sus scrofa in Western Europe, with particular reference to consumption of agricultural crops. *Mammal Review*, 33(1):43–56.

Schley, L., Dufrêne, M., Krier, A., and Frantz, A. C., 2008. Patterns of crop damage by wild boar (Sus scrofa) in Luxembourg over a 10-year period. *European Journal of Wildlife Research*, 54:589–599.

Senft, R. L., Coughenour, M. B., Bailey, D. W., Rittenhouse, L. R., Sala, O. E., and Swift, D. M., 1987. Large herbivore foraging and ecological hierarchies. *Bioscience*, 37(11). doi: 10.2307/1310545.

Singh, N. J., Börger, L., Dettki, H., Bunnefeld, N., and Ericsson, G., 2012. From migration to nomadism: movement variability in a northern ungulate across its latitudinal range. *Ecological Applications*, 22(7): 2007–2020. doi: 10.1890/12-0245.1.

Smith, H. G., Birkhofer, K., Clough, Y., Ekroos, J., Olsson, O., and Rundlöf, M., 2014. *Animal Movement Across Scales*, chapter Beyond dispersal: the role of animal movement in modern agricultural landscapes, pages 51–70. Oxford University Press.

Spitz, F. and Janeau, G., 1990. Spatial strategies: an attempt to classify daily movements of wild boar. *Acta Theriologica*, 35(1-2):129–149.

Sykes, N. and Putman, R., 2014. *Management of ungulates in the 21st century: how far have we come?*, page 304. Whittles Publishing, Dunbeath, Caithness, Scotland, UK.

Szemethy, L., Mátrai, K., Bíró, Z., and Katona, K., 2003. Seasonal home range shift of red deer in a forest-agriculture area in southern Hungary. *Acta Theriologica*, 48(4):547–556. doi: 10.1007/BF03192500.

Tallier, P.-A., 2004a. Chasse et forêts, forêt et chasses en Belgique, du XIXe au début du XXe siècle. Un couple incontournable et désastreux imposé par un statut social à acquérir ou à défendre. *Forêt Wallonne*, 71:12–25.

Tallier, P.-A., 2004b. Entre deboisements, boisement et reboisement, deux siècles d'histoire des forêts belges (1750-1950). *Forêt Wallonne*, 68:8–19.

Team, R. C., 2013. R: A language and environment for statistical computing. URL `http://www.R-project.org/`.

Thomas, C. D., Bodsworth, E. J., Wilson, R. J., Simmons, A. D., Davies, Z. G., Musche, M., and Conradt, L., 2001. Ecological and evolutionary processes at expanding range margins. *Nature*, 411(6837):577–581. doi: 10.1038/35079066.

Tolon, V., Dray, S., Loison, A., Zeileis, A., Fischer, C., and Baubet, E., 2009. Responding to spatial and temporal variations in predation risk: space use of a game species in a changing landscape of fear. *Canadian Journal of Zoology*, 87(12):1129–1137. doi: 10.1139/z09-101.

Toussaint, P. S. M. and Pirson, S., 2011. Les Néandertaliens du bassin mosan belge : bilan 2006-2011. *Bulletin des Chercheurs de la Wallonie*, hors-série n°4:149–196.

Tuomainen, U. and Candolin, U., 2011. Behavioural responses to human-induced environmental change. *Biological Reviews*, 86(3): 640–657. doi: 10.1111/j.1469-185X.2010.00164.x.

Turchin, P., 1998. *Quantitative Analysis of Movement: Measuring and Modeling Population Redistribution in Animals and Plants.* Sinauer Associates Inc., Sunderland, Massachusets.

Turchin, P., 1991. Translating Foraging Movements in Heterogeneous Environments into the Spatial Distribution of Foragers. *Ecology*, 72 (4):1253–1266. doi: 10.2307/1941099.

van Beest, F. M. and Milner, J. M., 2013. Behavioural Responses to Thermal Conditions Affect Seasonal Mass Change in a Heat-Sensitive Northern Ungulate. *PLoS ONE*, 8(6):e65972. doi: 10.1371/journal.pone.0065972.

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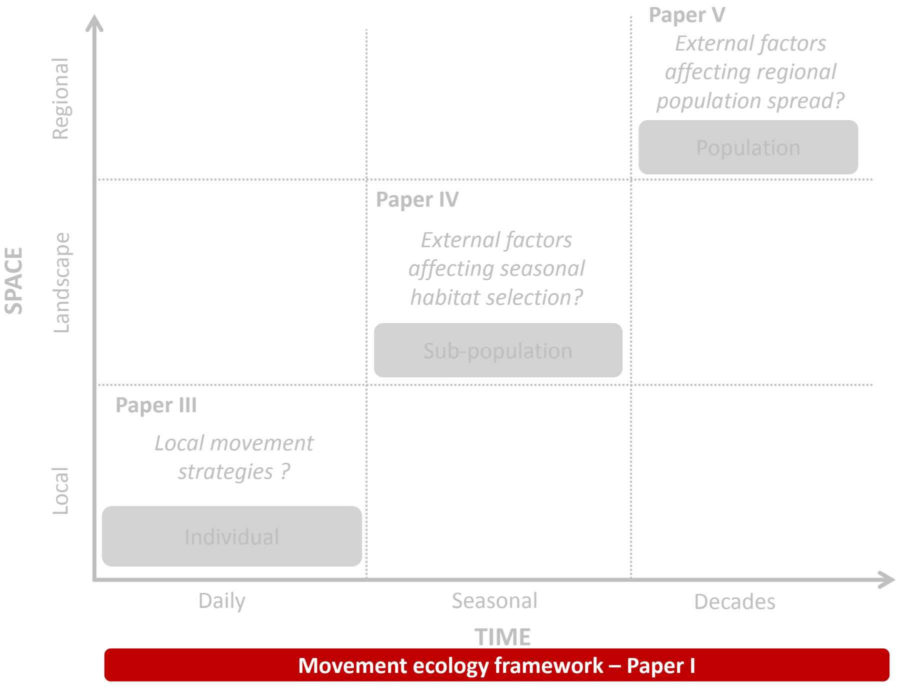
APPENDIX

A.1 PAPER I



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Is wild boar heading towards movement ecology? A review of trends and gaps

Kevin Morelle, François Lehaire and Philippe Lejeune

K. Morelle (morelle.k@gmail.com), F. Lehaire and P. Lejeune, Gembloux Agro Bio-Tech, Univ. of Liège, Passage des déportés 2, BE-5030 Gembloux, Belgium

Studies about the movement of mammals have recently gained much emphasis thanks to the development of new tracking technology, allowing highly accurate recording of animal movement. However, the amount of data made available requires effective theoretical and analytical framework for appropriate scientific use, i.e. to answer questions of interest. Within this review, we used systematic reviewing technique and the movement ecology framework to assess current knowledge and gaps in wild boar *Sus scrofa* spatial behaviour, species of high economic, ecological and social interest. Specifically, we observed that the development of new tracking techniques (radio-telemetry and global positioning system) has promoted movement-related studies since the early 2000. However, the ecology of movement, i.e. the why, how, when and where exactly an individual is moving is rarely the focus of these studies, which instead lies in the consequences of wild boar movement, e.g. the spread of disease, seed dispersal or damage. Most of the current studies are thus concerned with the interaction between environmental factors and spatial behaviour of the species, while other components of movement, internal state, navigation, and motion capacity are seldom studied. Compared to others ungulates, we also observed that wild boar movement ecology is still poorly considered in the literature. This review highlights the need for more quantitative descriptions of movement and behavioural-based approaches relating wild boar movement to its internal, navigational, and motion capacities. We expect that facilitated access to tracking technologies, in terms of cost and miniaturization, along with current interest in movement ecology will greatly promote increased knowledge in wild boar spatial behaviour.

Movement is the result of proximate and ultimate factors affecting individuals (Ferreras et al. 2004, Long et al. 2008). Proximate factors, via external (e.g. attraction to food resources or avoidance of a predator) or internal (e.g. sexes, development stages, energetic reserves) stimuli, contribute to specific spatial behaviours, while ultimate factors act under the yoke of evolutionary processes that select for behaviours that favour individuals with higher fitness, i.e. that increase the chances of survival and reproduction. Knowledge on movement of individuals can in turn help understanding and predicting population distribution, at a local, regional or biogeographical scale (MacArthur 1972, Pease et al. 1989, Cumming et al. 2012).

Considering the need for a unified theory and integrative paradigm for studies dealing with the movement of organisms, Nathan et al. (2008) have introduced a framework that is useful for exploring the causes, mechanisms, and patterns of movement at the individual, population or community scale. This conceptual framework defines the movement path of any mobile organism as the result of the interplay of four components: internal state, motion capacity, navigation capacity, and external factors (Fig. 1). Internal states refer to the physiological state and related motivation of the individual to move, which determines achievement of ultimate goals, e.g. gaining energy, seeking shelter, learning and reproduction (Martin et al. 2013). Motion capacity refers to the various ways, e.g. running, swimming and flying, an individual executes movement based on its biomechanical and morphological (Reilly et al. 2007). Navigation capacity describes the ability of the organism to orient in space and time given its cognitive or sensory abilities (Etienne et al. 1996). The last component of the framework, external factors, encompasses biotic and abiotic factors of the environment that can affect movement, such as habitat structure (Podgórski et al. 2013), ecological interactions (Keuling et al. 2008) or weather conditions (Lemel et al. 2003). This framework can serve as an effective starting point for observing the current knowledge of any species' movement ecology as it offers a particularly clear, coherent, and easy-to-use framework. For a complete description of the movement ecology paradigm, we refer the interested reader to the special feature of the Proceedings of the National Academy of Sciences journal which is freely accessible (Nathan 2008, Nathan et al. 2008).

Among the terrestrial mammal community, the Eurasian wild boar *Sus scrofa* has one of the largest geographic distribution (Oliver and Leus 2008). Thanks to their feeding (Schley and Roper 2003) and life history plasticity (Gamelon et al. 2013) they are able to cope with various environmental conditions (Podgórski et al. 2013).

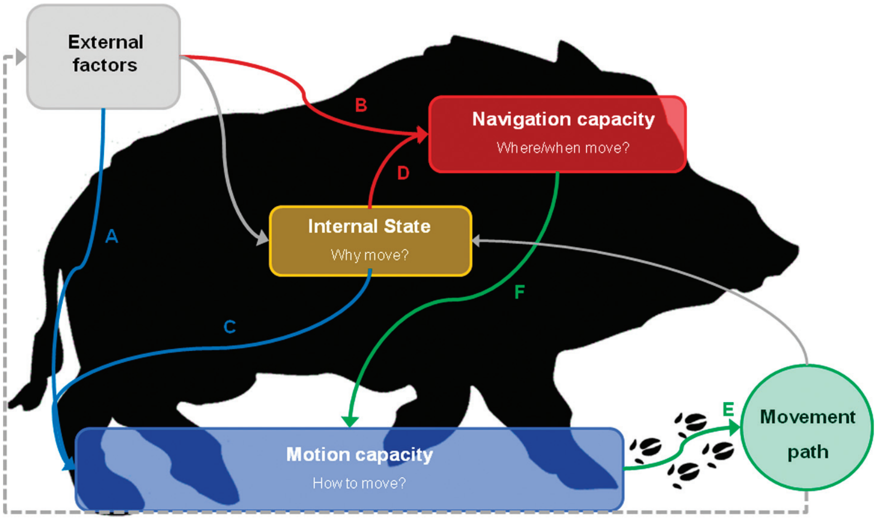

Figure 1. Illustration of the conceptual framework for movement ecology, adapted from Nathan et al. (2008). The framework is composed of four main components: internal state (physiological state affecting motivation to move), motion capacity (biomechanical or morphological properties of the individual enabling movement), navigation capacity (cues and sensory abilities used by the individual to move in space) and external factors (biotic and abiotic) affecting the animal movement. The result of the interactions between these four components is the movement path followed by the animal. The arrows indicate the different processes included in the movement: the motion process in blue (realized motion capacity resulting from the effect of external factors, internal state and the current location of the individual), the navigation process in red (realized navigation capacity resulting from the effect external factors, internal state and the current location of the individual), the movement propagation process in green (observed movement resulting from the motion and the navigation processes.

Worldwide their populations have hugely increased these last decades (Apollonio et al. 2010) due mainly to changes in farming practices, e.g. increase in maize cultivation area (Krüger 1998, Geisser and Reyer 2005) and land abandonment (García et al. 2006), milder winter condition (Melis et al. 2006), artificial feeding, and increase in mast frequency and abundance (Koenig and Knops 2000). Population increase combined with the plasticity of the species have facilitated the spread of the species within human-influenced habitats (agricultural land, peri-urban areas and abandoned industrial areas) where the animal bring up management (Kristiansson 1985, Hone 1995, Onida et al. 1995, Schley and Roper 2003, Geisser and Reyer 2004, Herrero et al. 2006, Schley et al. 2008), social (Cahill et al. 2012), and biodiversity (Galhano-Alves 2004) concerns. These concerns raise the need for more understanding of wild boar spatial ecology.

In this review, we aimed at describing and categorizing literature dealing with wild boar movement ecology, to better understand what has been studied and provide a map of movement ecology components and processes with well-studied areas and identified gaps. Our research question was thus relatively simple: What has been published about wild boar movement ecology and which components and processes of this framework have been considered so far? It is important to notice that with this review, we did not aim to consider the outcomes of the literature, but rather to gain a better understanding of the questions that have been tackled on the movement ecology of wild boar. To complete our literature mapping, we finally analysed position of wild boar in a broader context by comparing attention brought by movement ecology literature to wild boar with that brought to other ungulate species.

Material and methods

To scan and map the literature we used the techniques of systematic reviewing based on clear and explicit search terms method in a scientific database (Littell et al. 2008). A systematic review must be based on a 1) well-defined question, 2) search terms/criteria, 3) database searching procedure and 4) clear definition of exclusion/inclusion criteria (Lowry et al. 2012). To focus our review on papers dealing with movement ecology of wild boar, we adapted the search terms list used by Holyoak et al. (2008) (review on movement ecology across taxa) in combination with one of the four following words: 'wild boar', 'feral pig', 'feral hogs' or 'Sus scrofa' (Table 1). Next to the broad term 'movement', we used the following search terms to screen the database: dispersal, home range, spread, colonisation, expansion and migration. Applied to wild boar, 'dispersal' consists of natal and breeding dispersal, and refers respectively to movement of juveniles between the birth place and their first breeding site, and the inter breeding sites movement of individuals that have reproduced (Greenwood 1980). The 'home range' is the area used by an individual to meet its requirements in terms of growth (resource intake), reproduction, and survival (avoiding predation), although we found the recently proposed definition from Powell and Mitchell (2012) well adapted for wild boar: 'part of an animal's cognitive map of its environment that it chooses to keep updated'. 'Spread', 'colonisation' and 'expansion' are grouped together and refer to an increase in the area occupied by the species. They refer to large regional-scale movements and are most common in areas where wild boar have been reintroduced or exhibited a strong change in distribution (Erkinaro et al. 1982, Danilkin 2001). 'Migration' also covers large-scale movements and concerns mainly

Table 1. Terms used for the systematic search in the SCOPUS databank. The search procedure was: term 1 "AND" term 2, and when there was a third term, it was also with an "AND" and the semi-colon in term 3 indicates an "OR". For example, for the 6th search (= 6th line), the search was the following: (wild boar OR feral pig OR feral hog OR Sus scrofa) AND (Foraging) AND (gps OR telemetry OR migrat*). The "*" represented words with the preceding root, so that migrat* could represent any words with this root: migratory, migration, migrate, etc. The "?" in gene? flow represented both gene-flow and gene flow as both could be found in the literature.

Term 1	Term 2	Term 3
Wild boar; feral pig; feral hog, Sus scrofa	Telemetry	none
	Homing	none
	GPS	none
	Nomad*	none
	Dispersal	none
	Foraging	gps; telemetry; migrat*; ecosystem
	Orientation	gps, telemetry; migrat*; coloni*; expansion
	Movement*	forag*; gene flow; gps; radio; telemetry; migrat*; coloni*; spread*; population; habitat; mortality
	Gene?flow	behavi*; migrat*; expansion; colonization
	Migration	population; patch; individual; mortality; habitat; gps; telemetry; spread

seasonal movements away or back to new or established home range made by animals to cope with a change in food distribution or climatic conditions (Singer et al. 1981). We also included in the list the following terms: telemetry, homing, nomadism and foraging but compared with Holyoak et al. (2008), we added the terms 'GPS' and removed those not applicable to wild boar ('larva', 'pollen' and 'seed'). Within the SCOPUS database, we searched in titles, abstracts, or keywords, limiting our screening to the 'Life Sciences' subject areas and excluding literature from 'Physical Sciences', 'Health Sciences' and 'Social Sciences and Humanities'. The resulting 'hits' papers were then classified according to: 1) their general relevance to ecology; 2) the species of interest (single wild boar/feral pig species, multispecies or others species); 3) the research topic; and 4) their relevance in movement ecology (was movement focal or not?). A paper was considered as 'movement focal' if displacement of an individual or a population was clearly stated or measured (e.g. rate or distances) or could be inferred from the results (e.g. genetically related populations used as a proxy to infer movement between subpopulations). For example, we considered as movement focal, studies dealing with the use or effect of human infrastructures, e.g. road or wildlife passages crossing, and studies about historical analyses of population spread, e.g. archaeological observations of fossils. We did not consider as movement focal papers those dealing with the role of wild boar in disease spread, seed dispersal, and damage, unless movement was clearly measured, evaluated, or observed by any means. Papers in which wild or feral boar/hog/pig was the species of interest as well as papers considering multiple species, including wild boar, were considered for frequency terms analysis of words appearing within the abstract. Next, for papers in which movement was focal, we noted the method used to measure movement and the year the paper was published for temporal trends analysis. By careful reading of the abstract, we then classified movement focal papers according to the links of the movement ecology framework they consider (Fig. 2). Specifically, we defined the

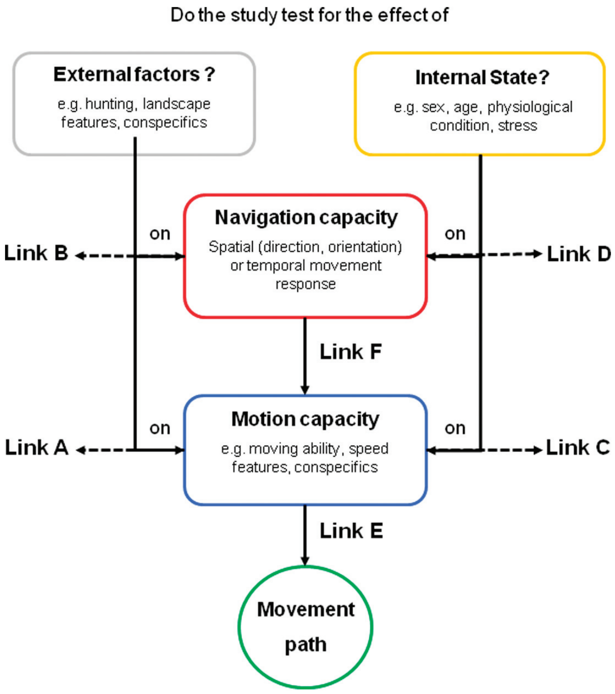

Figure 2. Schematic description of the method used to assess components and links of the movement ecology framework considered by the movement focal studies.

links within the movement ecology framework as follow: link A (external factors to motion capacity): studies considering the effect of external factors (biotic or abiotic) on the ability or way of moving (e.g. seasonal or hunting effects on home range size); link B (external factors to navigation capacity): studies considering the effect of external factors on the spatial (e.g. direction, orientation) or temporal (e.g. dispersal timing) movement response of the animal; link C (internal state to motion capacity): studies considering the role of the internal state (e.g. sex, age, physiological condition, stress) on the movement mode (e.g. speed) of the animal; link D (internal state to navigation capacity): studies considering the role of the internal state on the spatial or temporal movement response of the animal; link E (motion capacity to movement path): studies revealing movement occurrence but in which movement is not systematically measured, i.e. movement assessed qualitatively. Link F (navigation capacity to motion capacity): studies highlighting that navigation or orientation occurred without being related to external factors or internal state. When more than one link was considered in a paper, we counted it as many time. In most cases, the required information could be retrieved from the abstract but in cases where it was not possible, we examined the entire text of the article.

The last point of our review aimed at comparing movement ecology literature for wild boar and other common ungulates. For this part, we used Google scholar and compared the total number of hits for every selected species as well as the temporal evolution of this number. For every single ungulate species, we used the following search method: 'common name of the species' AND 'movement ecology'.

Results

The search in the SCOPUS database resulted in a total of 468 papers of which 34% were wild or feral boar-specific, 9% addressed multiple species including wild or feral boar, and 57% were related to other species. The low percentage of successful hits ($<50\%$) is explained by the high number of studies dealing with domestic pig *Sus scrofa domesticus* that were removed from subsequent analysis.

Word frequency analysis

For the frequency analysis, words were classified in five categories: 1) general terms used for describing movement; 2) the modes and/or patterns of movement; 3) external factors; 4) consequences of movement; and 5) other movement-related (Table 2). It revealed that the most frequent general terms were "movement" (appearing in 34.4% of studies), "gene flow" (23.3%), "dispersal" (17.8%), and "migration" (15.2%).

Modes and patterns of movement highlighted words such as "home range" (42.2%), "foraging" (45.6%), and "activity" split into seasonal (33.3%) and diel (26.7%) activity. "Ranging" and "habitat shift" appeared but less frequently, in 12.2% and 5.6% of the studies, respectively.

External factors were subdivided into four groups. In human-related factors, "hunting" (30.0%), "fences" (5.6%), "road" (10.0%), and "urban" (3.3%) were the most frequent words. Landscape-related words that appeared most frequently were related to "agriculture" (35.6%), "water" (22.2%), or "topography" (11.1%). The two last groups were predator-prey relationship (11.1%) and weather-related words (23.3%).

Table 2. Frequency table of the terms included in the abstract of the relevant papers.

	Frequency	Percent of studies
General terms for movement		
gene flow	68	23.3
movement	60	34.4
dispersal	52	17.8
migration	20	15.6
other general terms (mainly broad-scale movement)	83	42.2
Modes and patterns of movement		
home range	151	42.2
foraging	131	45.6
seasonal activity	124	33.3
diel activity	52	26.7
habitat shift	15	5.6
ranging	12	12.2
other modes/patterns-1	34	21.1
External factors		
Human-related		
hunting	137	30.0
fence	35	5.6
road	21	10.0
urban	7	3.3
Landscape-related		
agricultural	114	35.6
Water-related terms	53	22.2
topography	19	11.1
other landscape elements	38	20.0
Predator–prey	38	11.1
Weather-related	55	23.3
Consequences of movement		
disease	125	28.9
seed dispersal	42	12.2
damage	16	10.0
disturbance	10	6.7
economic losses	7	6.7
Other related words		
population	138	61.1
radiotelemetry	107	54.4
management-control	96	43.3
density	65	28.9
distance	44	25.6
distribution	43	28.9

In the *consequences of movement* category, the words "disease" (28.9%), "seed dispersal" (12.2%), "damage" (10.0%), "disturbances" (6.7%), and "economic loss" (6.7%) were the most common.

In the *other words* category, words "population" (61.1%), "radiotelemetry" (54.4%), "management-control" (43.3%), "density" (28.9%), "distance" (25.6%), and "distribution" (28.9%) were the most frequent.

Comparison between movement focal and not focal studies highlighted important differences in the most frequent words (Fig. 3). In movement focal studies (Fig. 3, upper part), frequent terms were more related to the invasive character of the species ("feral", "pigs"), and the scale of study investigation ("home", "range", "population"). In contrast,

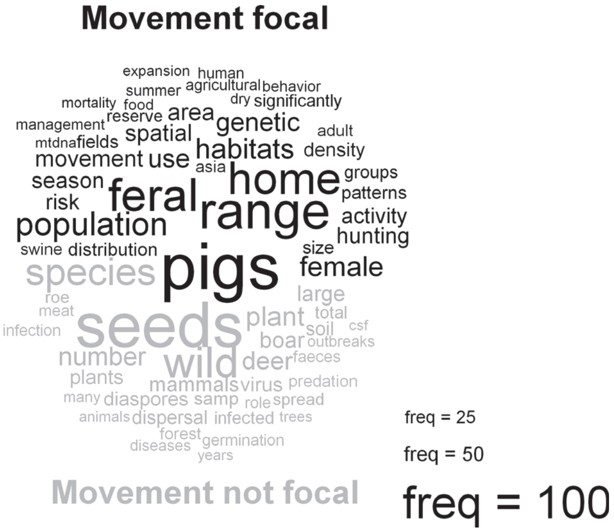

Figure 3. Word cloud representing the 70 most frequent words in the abstract of the 'hit' papers. In the upper part (black) are words related to the movement focal studies, and in the lower part (grey) are words related to wild boar but where movement was not focal to the study. As indicated by the frequency with which a word appears in the title, abstract and keywords of the papers.

studies where movement was not focal (Fig. 3, lower part) highlighted mostly the role of wild boar as a seeds disperser ("seeds", "plants") and as a vector for diseases ("virus", "outbreak", "infected").

Movement focal analysis

The next results considered movement focal studies, made of a corpus of 101 papers. Unsurprisingly among these studies, the most common method used for measuring movement was telemetry (42.7% of the studies), split into radio-telemetry with 30.0% and GPS with 12.7% of studies. This means that more than half of movement focal publications did not use radio or GPS tracking method. Among other methods used, capture–recapture studies accounted for 4.5%. Indirect measures of wild boar movement were obtained by means of genetic analyses (15.5%), ground surveys (17.3%), and model-based approaches (8.2%). Other, more marginal methods included archaeological search, isotope analysis, review of the literature and questionnaire.

Temporal trends revealed that the observed increase in the number of movement focal studies was linked to the increased use of radio and GPS-tracking methods (Fig. 4). During the period 1980–2012, we observed a mean annual increase rate of 12.4%.

Movement ecology framework

Link E, expressing the relation between motion capacity of the animal and movement path, was addressed in 96% of studies (Fig. 5). It relates mostly to genetic studies, such as the one from Watanobe et al. (2003) in which the

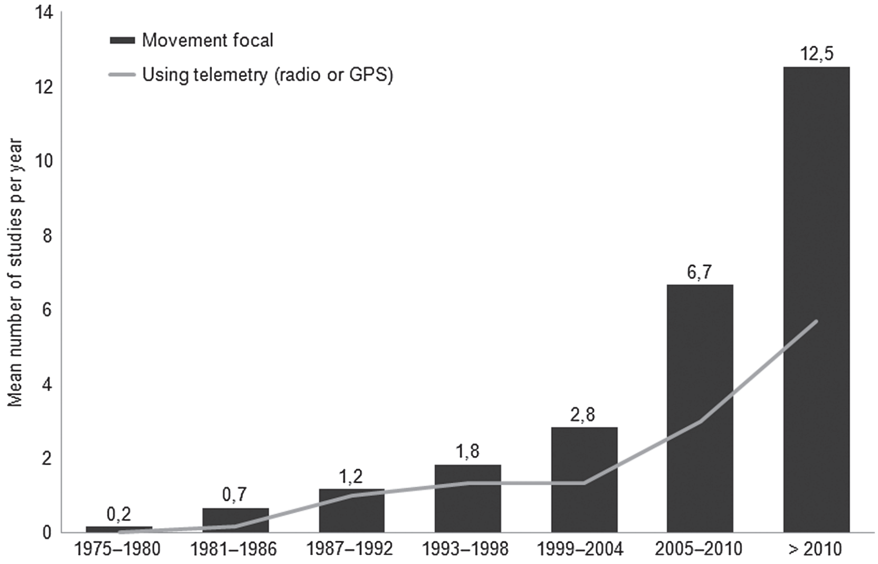

Figure 4. Temporal evolution of the number of movement focal studies (black bar) and those based on telemetry tracking methods (grey line).

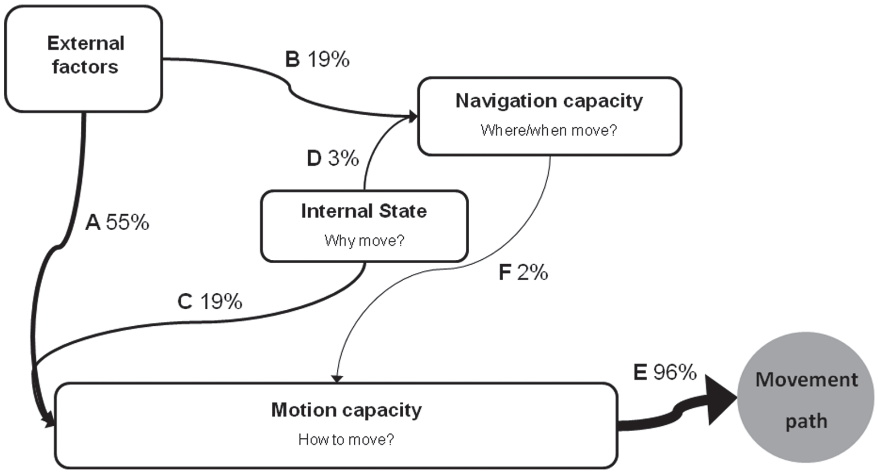

Figure 5. Percentage of studies per link between components of the movement ecology framework. An example of link A is a study on the effect of season on the movement pattern (feeding and exploring) and rate (mean distance walked) of wild pigs. An example of link B is a study on the effect of geographic features (hydrographic network) on the migration ability and the distribution of a sub-population. An example of link C is a study on the effect of sex on the movement rate between resting sites. An example of link D is a study on the effect of age and sex on the dispersal distance to capture site. An example of link E is a study that investigates the genetic relationship between wild boar and domestic pigs, highlighting human-induced displacement, but confirming that movement occurred. An example of link F is a study on anisotropy in direction of recaptures events and home range shape, demonstrating that navigation or orientation occurred.

migration distance (motion capacity) and the movement path of wild boar is inferred from genetic comparison of geographically distant populations. Link between external factors and motion capacity was the second most considered link (A, 55% of studies). Example of link A study is the study from Podgórski et al. (2013), demonstrating among others the effect of human presence and habitat structure (the external factors) on the travelling speed (how to move?, motion capacity) or the one by Hone and Atkinson (1983) that studied the effect of different fences types (the external factor) on the ability of feral pigs to move between paddocks. Link B was studied in 19% of cases. Example for link B is a study about the effect of human presence on the directional response of the wild boar (Marini et al. 2009). The internal state of wild boar was considered in 22% of cases, more specifically its effect on motion capacity (link C, 19% of cases) and on navigation capacity (link D, 3% of cases). Most of these studies considering internal state referred to developmental stage or sex difference effect on movement, e.g. study by Keuling et al. (2010) for link D or Janeau et al. (1995) for link C. The link F between navigation and orientation mechanisms was considered in only 2% of studies.

Ungulates and movement ecology

Comparison of the importance of movement ecology between wild boar and other ungulates species showed that wild boar belongs to the group of ungulates species with the least interest, as it can be observed on the Table 3 showing the total number of hits for the search combining the common name of the species and "movement ecology". Compared to elk, moose, red deer or roe deer, there are respectively 7, 5, 4 and 3 times less publications on movement ecology for wild boar (Table 3). Temporal analysis revealed an increase in the number of movement ecology publications for most of the ungulates species since the early 2000, helped by seminal papers in movement ecology by Holden (2006) and Nathan et al. (2008). In contrast, publications concerning wild boar movement ecology hardly follow this upward trend though we can notice a slight increase since 1990 (Fig. 6).

Discussion

This review aimed to investigate how the ecology of movement of wild boar was considered in the scientific literature.

Table 3. Comparison between the number of Google scholar hits for different ungulates species. Search terms used were the following: "the common name of the species" AND "movement ecology".

Species	No. of hits
Elk *Cervus canadensis*	267
White-tailed deer *Odocoileus virginianus*	227
Moose *Alces alces*	171
Caribou *Rangifer tarandus granti*	165
Red deer *Cervus elaphus*	127
Mule deer *Odocoileus hemionus*	124
Roe deer *Capreolus capreolus*	93
Zebra *Equus burchelli*	91
Bison *Bison bison*	80
Wildebeest *Connochaetes taurinus*	71
Reindeer *Rangifer tarandus*	67
Bighorn sheep *Ovis canadensis*	54
Pronghorn *Antilocapra americana*	40
African buffalo *Syncerus caffer*	40
Wild boar *Sus scrofa*	**36**
Mountain goat *Oreamnos americanus*	12
Soay sheep *Ovis aries*	10
Alpine ibex *Capra ibex*	6
Greater kudu *Tragelaphus strepsiceros*	4
Feral horse *Equus caballus*	3
Dall sheep *Ovis dalli*	2
Chillingham cattle *Bos taurus*	1

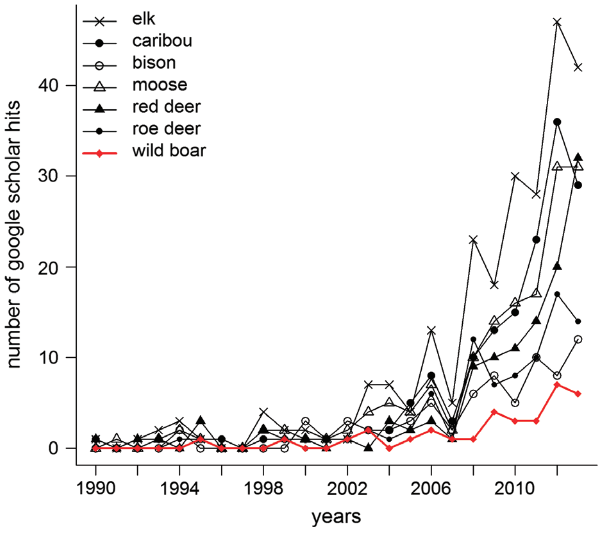

Figure 6. Evolution of the number of hits resulting from a Google scholar search about different ungulates species and movement ecology. For every of these species, we used the following search terms: "common name of the species" AND "movement ecology".

The words frequency analysis showed that many studies have focused on large-scale processes, e.g. gene flow between subpopulations. Although movement is generally not their central goal, these studies are of high interest to demonstrate the role of environmental and human-related features on the dispersal or migratory patterns of wild boar (Cowled et al. 2008). However, because these studies are made over large geographical scale at the population level, they lack detailed information on navigation capacity, motion capacity, and readiness to move and their interactions. Modes and patterns of movement addressed mostly in first place home range and foraging studies, tending to prove that what came under 'movement ecology' is still mostly habitat- and resources-related (McIlroy 1989, Xu et al. 2011, Wurster et al. 2012). Most research indeed studied what habitat type are preferred by wild boar and how they use them (Cahill et al. 2003, Hayes et al. 2009) rather then the way they move between and within these habitats. Though, we did not include 'activity' as a search terms, we observed high occurrences of papers dealing with activity patterns, defined here as the percent of active time (Massei et al. 1997), demonstrating the close relationship between movement and activity. It also highlights the likely mismatch in the use of these terms. Indeed, when considered in parallel to movement, activity, usually measured by means of a sensor integrated into telemetry devices, offers the opportunity to disentangle the behaviour, resting, lying, feeding, and moving (Massei et al. 1997), likely explanations why most studies dealing with activity patterns of animals refer in some way to movement. Foraging is also an important movement-related term and is generally studied under the frame of damage or potential threats brought by wild boar to vegetation or agriculture (Nogueira-Filho et al. 2009). Habitat shift and ranging behaviour are other relevant characteristics of the spatial strategies used by wild boar (Spitz and Janeau 1990, Keuling et al. 2009). External factors showed that the species and its interaction with humans is an increasing concern and is widely related to barriers to movement at lower, e.g. fences (Reidy et al. 2008), and larger scales, e.g. roads and highways (Woess et al. 2002), though wild boar demonstrate abilities to cope with these infrastructures (Frantz et al. 2012).

Wild boar is also largely studied for its negative impacts, e.g. disease spread, disease transmission to livestock (Serraino et al. 1999) or domestic pigs (Fritzemeier et al. 2000, Zanardi et al. 2003, Boklund et al. 2008), and damage to agriculture (Schley et al. 2008). However, the positive effect of wild boar on other organisms (plants and invertebrates), dispersal via both epi- and endozoochory, is more and more studied (Heinken et al. 2001, Schmidt et al. 2004). As an illustration, although we removed the term 'seeds' from the literature search, many studies about seeds dispersal were found with the systematic review, highlighting the growing importance for studies on the role of mammals in forest spatial dynamics and structure (Heinken et al. 2006), but also in the propagation of exotic or invasive plants (Dovrat et al. 2012). In this sense, the movement ecology framework is also opportune as it helps to consider multiple-species-based processes and interactions (Tsoar et al. 2011). For example, wild boar considered in a seed dispersal study becomes part of the motion capacity of the plants it transports (Matias et al. 2010).

To make sense, the differences in spatial scales of the analyses related above have to be linked to the level at which the species was considered: were individuals or part of the entire population the subject of analysis? Here the papers found via the search terms method included both population- and individual-based studies, so that the level at which analyses were performed ranged from experimental studies, based on few individuals, e.g. impact of fences on movement (Reidy et al. 2008), to regional and population level studies, e.g. genetic analyses (Spencer and Hampton 2005, Iacolina et al. 2009). The level of analysis was mostly dependent on the techniques used, i.e. genetic-based studies focus on the population scale and with tracking techniques on individuals, a scale-dependent type of movement and research question can be investigated. More and more, however, we observed a positive trend towards greater use of individual-tracking methods, revealing increasing awareness of the importance of considering individual variation in movement. This variation, coming from age, sex, genetics, or experience, has been shown recently to be one of the main factors to consider for inference analysis of the role of navigation and motion capacity in movement ecology (Hawkes 2009). With the development of telemetry technology, more accurate and recursive position data can now be acquired in the field (Baubet et al. 2003). Advanced tracking techniques are indeed more and more accessible and used, and the next step will bring researchers towards the use of bio-loggers. Compared with traditional tracking devices, bio-loggers include equipment able to retrieve information about the animal's physiology (e.g. stress, temperature, and pulse), allowing researchers to go deeper in the understanding of the readiness of an animal to move.

Compared to Holyoak et al. (2008), we obtained similar percentage of studies in the different links of the movement ecology framework, with the following order of importance: link E > link A > link B = link C. Difference appears for link D (3% versus 2% in the study by Holyoak et al.) and link F (2% versus 12%). As expected, a vast majority (link

E 96%, Fig. 5) of the movement focal studies did report occurrence or measurement of movement. The similarities allows us to extend to wild boar the observations made by Holyoak et al. (2008) that external factors is the component of the movement ecology framework the most considered. This could be explained by the methods used that operate over a large scale such as molecular genetic tools, which allows researchers to consider more easily this component. Including external factors in the research, e.g. via extraction of information or metrics from an environmental map with geographic information system (GIS) tools, is also more affordable for scientist than considering physiological condition of an individual for example. As shown by Holyoak et al. (2008) for vertebrates, the effect of external factors on motion capacity of wild boar (link A) was considered in more than half of the studies. Questions tackled in these studies concern the influence of biotic, e.g. other species (Ilse and Hellgren 1995) or abiotic (Hone and Atkinson 1983, Woess et al. 2002) factors on the ability to move. Internal state component was addressed in slightly more than 20% of the studies. Generally these studies analysed spatial behaviour differences between sex (Dexter 1998) or developmental stage (Janeau et al. 1995). Studying internal state remains dependent on methods able to consider the animal's physiology or cognition. Link F and D with respectively 2 and 3% of frequency in the movement focal studies were the least consider links of the framework. Most likely explanation for this is that these links concern navigation capacity for which knowledge about the use of cues or memory to orient and navigate in space is required but which is probably the most difficult to assess in the wild and require experimental observation (Croney et al. 2003).

Our results have shown that studies dealing with spatial ecology of other ungulates, e.g. moose (Morales et al. 2005, Leblond et al. 2010), caribou (Semeniuk et al. 2012), and elk (Morales et al. 2005), are much more numerous than for wild boar. Why this difference? The relative difficulty of fitting wild boar with a telemetry collar because of the absence of a neck such as in other ungulates species makes wild boar not the ideal candidate species for GPS technology. Moreover, material issues, e.g. collar malfunctions because of battery or hardware failure and cost of the GPS devices, can partly explain this phenomenon. Wyckoff et al. (2007) have experienced more than 50% failure rate in collar performance and 20% of collars slipped off while tracking feral swine in Texas. Still, collaring wild boar is possible and likely progress in the development of tracking devices (via miniaturisation, e.g. ear tag) will make wild boar an even better candidate for movement ecology studies. These new biotelemetry techniques, used in combination with indirect measures of movement (molecular genetics and stable isotope tracers), could bring up interesting and complementary information about an animal's movement. Compared to other ungulate species, wild boar also present the 'disadvantage' of being omnivorous which could make the species not as 'attractive' biological model as other species for movement ecologists, because quantification of resource and understanding of predictions and hypotheses about foraging tactics are not facilitated for the study of generalist species. As a consequence, there's a current lack of a very large database of localisations, compared with other ungulates for which radio and GPS track research was started decades earlier (Hawkins and Montgomery 1969).

We found many papers in our review that dealt with more than one component at the same time, e.g. a study considering both the effect of conspecifics (external factors) and age-sex (internal state) on movement within and between groups of wild boar (Hirotani and Nakatani 1987). Maybe it would have been interesting to classify the studies under the view of a panel of experts, as Holyoak et al. (2008) did, to obtain a mean response that is probably closer to the reality. We proposed that studies considering the movement of organisms in their research should more clearly state the components and interactions investigated in the study.

Another limitation of this review is that the terms search method used here prevented us from being exhaustive, so that a large part of the scientific literature dealing with wild boar and movement remained unconsidered by this selection process. We suggest that this quantitative review could be extended purposely with a more exhaustive literature search. Such a review of the literature would bring more insight into movement ecology of the species rather than a literature trend.

Wild boar is able of complex spatial behaviour and we need analytical as well as mechanistic movement models that could help us understand their behaviour. Movement ecology framework provides such a tool that enables scientists to study the causes, mechanisms, and patterns of organisms' movement with a common conceptual framework. We used this framework as a reviewing tool but it could also be adapted purposely to develop meta-analysis studies, researches on missing links of movement ecology, e.g. C, D, F in the case of wild boar, or simply to get an overall understanding of movements of any mobile organism. In this sense, we encourage researchers working in the field of movement ecology to consider their species, guild or community of interest under the prism of this framework. Using a common structure would indeed greatly facilitate comparison of results among studies and enable the development of fruitful intra- and inter-specifics comparative studies.

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References

Apollonio, M. et al. (eds) 2010. European ungulates and their management in the 21st century. – Cambridge Univ. Press.

Baubet, E. et al. 2003. Can wild boar be surveyed using GPS? – Mem. Natl Inst. Polar Res. 58: 188–195.

Boklund, A. et al. 2008. Simulating the spread of classical swine fever virus between a hypothetical wild-boar population and domestic pig herds in Denmark. – Preventive Vet. Med. 85: 187–206.

Cahill, S. et al. 2003. Spacing and nocturnal activity of wild boar *Sus scrofa* in a Mediterranean metropolitan park. – Wildlife Biol. 9: 3–13.

Cahill, S. et al. 2012. Characteristics of wild boar (*Sus scrofa*) habituation to urban areas in the Collserola Natural Park (Barcelona) and comparison with other locations. – Anim. Biodivers. Conserv. 35: 221–233.

Cowled, B. et al. 2008. Feral pig population structuring in the rangelands of eastern Australia: applications for designing adaptive management units. – Conserv. Genet. 9: 211–224.

Croney, C. C. et al. 2003. A note on visual, olfactory and spatial cue use in foraging behavior of pigs: indirectly assessing cognitive abilities. – Appl. Anim. Behav. Sci. 83: 303–308.

Cumming, G. S. et al. 2012. Towards a unification of movement ecology and biogeography: conceptual framework and a case study on Afrotropical ducks. – J. Biogeogr. 39: 1401–1411.

Danilkin, A. A. 2001. The wild boar: an unprecedented spread or restoration of the species range? – Doklady Biol. Sci. 380: 457–460.

Dexter, N. 1998. The influence of pasture distribution and temperature on habitat selection by feral pigs in a semi-arid environment. – Wildlife Res. 25: 547–559.

Dovrat, G. et al. 2012. Wild boars as seed dispersal agents of exotic plants from agricultural lands to conservation areas. – J. Arid Environ. 78: 49–54.

Erkinaro, E. et al. 1982. Occurence and spread of the wild boar (*Sus scrofa*) in eastern Fennoscandia. – Memoranda 58: 39–47.

Etienne, A. S. et al. 1996. Path integration in mammals and its interaction with visual landmarks. – J. Exp. Biol. 199: 201–209.

Ferreras, P. et al. 2004. Proximate and ultimate causes of dispersal in the Iberian lynx *Lynx pardinus*. – Behav. Ecol. 15: 31–40.

Frantz, A. C. et al. 2012. Comparative landscape genetic analyses show a Belgian motorway to be a gene flow barrier for red deer (*Cervus elaphus*), but not wild boars (*Sus scrofa*). – Mol. Ecol. 21: 3445–3457.

Fritzemeier, J. et al. 2000. Epidemiology of classical swine fever in Germany in the 1990s. – Vet. Microbiol. 77: 29–41.

Galhano-Alves, J. P. O. 2004. Man and wild boar: a study in Montesinho Natural Park, Portugal. – Galemys 16: 223–230.

Gamelon, M. et al. 2013. Fluctuating food resources influence developmental plasticity in wild boar. – Biol. Lett. 9: 20130419.

García, D. J. et al. 2006. Relationship between game species and landscape structure in the SE of Spain. – Wildilfe Biol. Practice 2: 48–62.

Geisser, H. and Reyer, H.-U. 2004. Efficacy of hunting, feeding and fencing to reduce crop damage by wild boars. – J. Wildlife Manage. 68: 939–946.

Geisser, H. and Reyer, H.-U. 2005. The influence of food and temperature on population density of wild boar *Sus scrofa* in the Thurgau (Switzerland). – J. Zool. 267: 89–96.

Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. – Anim. Behav. 28: 1140–1162.

Hawkes, C. 2009. Linking movement behaviour, dispersal and population processes: is individual variation a key? – J. Anim. Ecol. 78: 894–906.

Hawkins, R. E. and Montgomery, G. G. 1969. Movements of translocated deer as determined by telemetry. – J. Wildlife Manage. 33: 196–203.

Hayes, R. et al. 2009. Survival and habitat use of feral hogs in Mississippi. – Southeastern Nat. 8: 411–426.

Heinken, T. et al. 2001. Welche Rolle spielt die endozoochore Ausbreitung von Pflanzen durch wildlebende Säugetiere? - Untersuchungen in zwei brandenburgischen Waldgebieten. – Hercynia N.F 34: 237–259.

Heinken, T. et al. 2006. Soil seed banks near rubbing trees indicate dispersal of plant species into forests by wild boar. – Basic Appl. Ecol. 7: 31–44.

Herrero, J. et al. 2006. Diet of wild boar *Sus scrofa* L. and crop damage in an intensive agroecosystem. – Eur. J. Wildlife Res. 52: 245–250.

Hirotani, A. and Nakatani, J. 1987. Grouping-patterns and intergroup relationships of Japanese wild boars (*Sus scrofa leucomystax*) in the Rokko mountain area. – Ecol. Res. 2: 77–84.

Holden, C. 2006. Inching toward movement ecology. – Science 313: 779–782.

Holyoak, M. et al. 2008. Trends and missing parts in the study of movement ecology. – Proc. Natl Acad. Sci. USA 105: 19060–19065.

Hone, J. 1995. Spatial and temporal aspects of vertebrate pest damage with emphasis on feral pigs. – J. Appl. Ecol. 32: 311–319.

Hone, J. and Atkinson, B. 1983. Evaluation of fencing to control feral pig movement. – Aust. Wildlife Res. 10: 499–505.

Iacolina, L. et al. 2009. Nonkin associations in wild boar social units. – J. Mammal. 90: 666–674.

Ilse, L. M. and Hellgren, E. C. 1995. Spatial use and group dynamics of sympatric collared peccaries and feral hogs in southern Texas. – J. Mammal. 76: 993–1002.

Janeau, G. et al. 1995. Role of daily movements in the sociospatial organization of wild boar populations (*Sus scrofa* L.). – Rev. d'Ecol. Terre Vie 50: 35–48.

Keuling, O. et al. 2008. How does hunting influence activity and spatial usage in wild boar *Sus scrofa* L.? – Eur. J. Wildlife Res. 54: 729–737.

Keuling, O. et al. 2009. Commuting, shifting or remaining? Different spatial utilisation patternsof wild boar *Sus scrofa* L. in forest and field crops during summer. – Mammal. Biol. 74: 145–152.

Keuling, O. et al. 2010. Hunter feedback of individually marked wild boar *Sus scrofa* L.: dispersal and efficiency of hunting in northeastern Germany. – Eur. J. Wildlife Res. 56: 159–167.

Koenig, W. D. and Knops, J. M. H. 2000. Patterns of annual seed production by northern hemisphere trees: a global perspective. – Am. Nat. 155: 59–69.

Kristiansson, H. 1985. Crop damage by wild boars in central Sweden. – In: de Crombrugghe, S. A. (ed.), Proc. 17th Congr. IUGB,Brussels, pp. 605–609.

Krüger, T. 1998. Entwicklung der Jagdstrecken des Schwarzwildes (*Sus scrofa* L. 1758) und möglicher Einfluissfaktoren im heutigen Freistaat Sachsen. – Z. Jagdwissenschaft 44: 151–166.

Leblond, M. et al. 2010. What drives fine-scale movements of large herbivores? A case study using moose. – Ecography 33: 1102–1112.

Lemel, J. et al. 2003. Variation in ranging and activity behaviour of European wild boar *Sus scrofa* in Sweden. – Wildlife Biol. 9: 29–36.

Littell, J. H. et al. 2008. Systematic reviews and meta analysis. – Oxford Univ. Press.

Long, E. S. et al. 2008. Multiple proximate and ultimate causes of natal dispersal in white-tailed deer. – Behav. Ecol. 19: 1235–1242.

Lowry, E. et al. 2012. Biological invasions: a field synopsis, systematic review, and database of the literature. – Ecol. Evol. 3: 182–196.

MacArthur, R. H. 1972. Geographical ecology: patterns in the distribution of species. – Princeton Univ. Press

Marini, F. et al. 2009. Response to human presence during nocturnal line transect surveys in fallow deer (*Dama dama*) and wild boar (*Sus scrofa*). – Eur. J. Wildlife Res. 55: 107–115.

Martin, J. et al. 2013. Reciprocal modulation of internal and external factors determines individual movements. – J. Anim. Ecol. 82: 290–300.

Massei, G. et al. 1997. Factors influencing home range and activity of wild boar (*Sus scrofa*) in a Mediterranean coastal area. – J. Zool. 242: 411–423.

Matias, L. et al. 2010. Seed dispersal patterns by large frugivorous mammals in a degraded mosaic landscape. – Restor. Ecol. 18: 619–627.

McIlroy, J. C. 1989. Aspects of the ecology of feral pigs *(Sus scrofa)* in the Murchison area; New Zealand. – N. Z. J. Ecol. 12: 11–22.

Melis, C. et al. 2006. Biogeographical variation in the population density of wild boar (*Sus scrofa*) in western Eurasia. – J. Biogeogr. 33: 803–811.

Morales, J. M. et al. 2005. Adaptive models for large herbivore movements in heterogeneous landscapes. – Landscape Ecol. 20: 301–316.

Nathan, R. 2008. An emerging movement ecology paradigm. – Proc. Natl Acad. Sci. USA 105: 19050–19051.

Nathan, R. et al. 2008. A movement ecology paradigm for unifying organismal movement research. – Proc. Natl Acad. Sci. USA 105: 19052–19059.

Nogueira-Filho, S. G. et al. 2009. Ecological impacts of feral pigs in the Hawaiian Islands. – Biodivers. Conserv. 18: 3677–3683.

Oliver, W. and Leus, K. 2008. *Sus scrofa*. – In: IUCN 2013. IUCN red list of threatened species. Ver. 2013.2. <www.iucnredlist.org>. Downloaded on 20 January 2014.

Onida, P. et al. 1995. Damages caused to crops by wild boar (*S. scrofa meridionalis*) in Sardinia (Italy). – Ibex J. Mountain Ecol. 3: 230–235.

Pease, C. M. et al. 1989. A model of population growth, dispersal and evolution in a changing environment. – Ecology 70: 1657–1664.

Podgórski, T. et al. 2013. Spatiotemporal behavioral plasticity of wild boar (*Sus scrofa*) under contrasting conditions of human pressure: primeval forest and metropolitan area. – J. Mammal. 94: 109–119.

Powell, R. A. and Mitchell, M. S. 2012. What is a home range? – J. Mammal. 93: 948–958.

Reidy, M. M. et al. 2008. Evaluation of electric fencing to inhibit feral pig movements. – J. Wildlife Manage. 72: 1012–1018.

Reilly, S. M. et al. 2007. Posture, gait and the ecological relevance of locomotor costs and energy-saving mechanisms in tetrapods. – Zoology 110: 271–289.

Schley, L. and Roper, T. J. 2003. Diet of wild boar *Sus scrofa* in western Europe, with particular reference to consumption of agricultural crops. – Mammal Rev. 33: 43–56.

Schley, L. et al. 2008. Patterns of crop damage by wild boar (*Sus scrofa*) in Luxembourg over a 10-year period. – Eur. J. Wildlife Res. 54 589–599.

Schmidt, M. et al. 2004. Dispersal of vascular plants by game in northern Germany. Part I: Roe deer (*Capreolus capreolus*) and wild boar (*Sus scrofa*). – Eur. J. For. Res. 123: 167–176.

Semeniuk, C. A. D. et al. 2012. Incorporating behavioral–ecological strategies in pattern-oriented modeling of caribou habitat use in a highly industrialized landscape. – Ecol. Modell. 243: 18–32.

Serraino, A. et al. 1999. Monitoring of transmission of tuberculosis between wild boars and cattle: genotypical analysis of strains by molecular epidemiology techniques. – J. Clinical Microbiol. 37: 2766–2771.

Singer, F. J. et al. 1981. Home ranges, movements, and habitat use of european wild boar in Tennessee. – J. Wildlife Manage. 45: 343–353.

Spencer, P. B. S. and Hampton, J. O. 2005. Illegal translocation and genetic structure of feral pigs in Western Australia. – J. Wildlife Manage. 69: 377–384.

Spitz, F. and Janeau, G. 1990. Spatial strategies: an attempt to classify daily movements of wild boar. – Acta Theriol. 35: 129–149.

Tsoar, A. et al. 2011. A movement ecology approach to study seed dispersal and plant invasion: an overview and application of seed dispersal by fruit bats. – In: Richardson, D. M. (ed.), Fifty years of invasion ecology: the legacy of Charles Elton. Wiley, pp. 103–119.

Watanobe, T. et al. 2003. Phylogeography and population structure of the Japanese wild boar *Sus scrofa leucomystax*: mitochondrial DNA variation. – Zool. Sci. 20: 1477–1489.

Woess, M. et al. 2002. Green bridges and wildlife corridors in Austria. – Z. Jagdwissenschaft 48: 25–32.

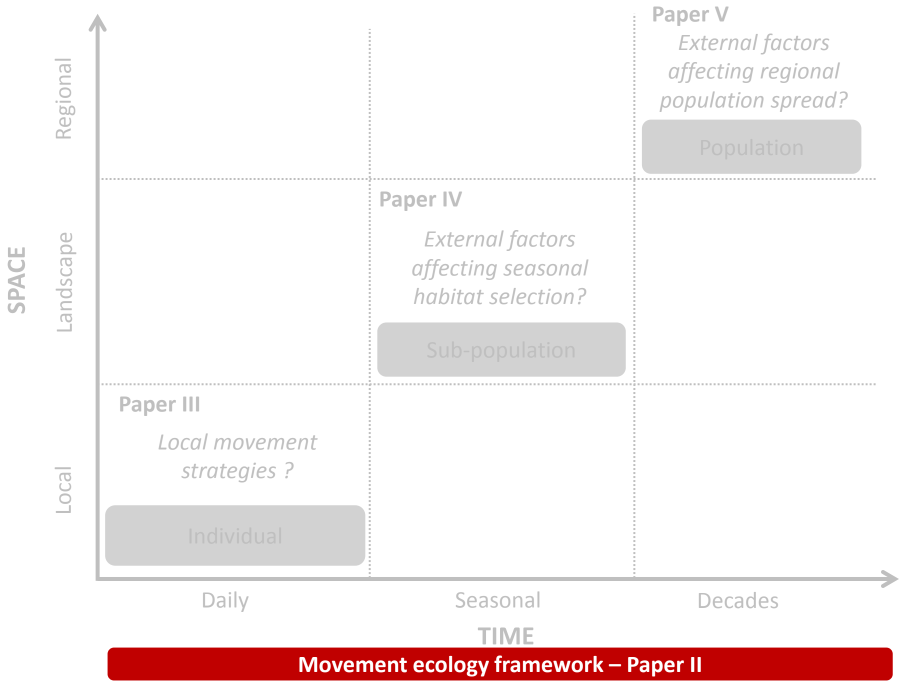
Wurster, C. M. et al. 2012. Utilization of sugarcane habitat by feral pig (*Sus scrofa*) in northern tropical Queensland: evidence from the stable isotope composition of hair. – PLoS ONE 7(9): e43538.

Wyckoff, C. et al. 2007. Gps telemetry collars: considerations before you open your wallet. – In: Nolte, D. L. et al. (eds), Proc. 12th Wildlife Damage Management Conf., pp. 571–576.

Xu, F. et al. 2011. Autumn habitat selection of wild boar in the Fenghuangshan Nature Reserve, Heilongjiang Province. – Beijing Linye Daxue Xuebao/J. Beijing For. Univ. 33: 86–91.

Zanardi, G. et al. 2003. Classical swine fever in wild boar in the Lombardy region of Italy from 1997 to 2002. – Vet. Record 152: 461–465.

A.2 PAPER II



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REVIEW

Towards understanding wild boar *Sus scrofa* movement: a synthetic movement ecology approach

Kevin MORELLE* *Department of Forest and Nature Management, Gembloux Agro Bio-Tech, University of Liège, Passage des déportés 2, 5030 Gembloux, Belgium. E-mail: morelle.k@gmail.com*
Tomasz PODGÓRSKI *Mammal Research Institute, Polish Academy of Sciences, ul. Waszkiewicza 1, 17-230 Białowieża, Poland. E-mail: t_podgorski@ibs.bialowieza.pl*
Céline PRÉVOT *Department of Natural and Agricultural Environmental Studies, Service Public de Wallonie, Avenue Maréchal Juin 23, 5030 Gembloux, Belgium. E-mail: Celine.prevot@spw.wallonie.be*
Oliver KEULING *Institute for Terrestrial and Aquatic Wildlife Research, University of Veterinary Medicine, Bischofholer Damm 15, 30173 Hannover, Germany. E-mail: Oliver.Keuling@tiho-hannover.de*
François LEHAIRE *Department of Forest and Nature Management, Gembloux Agro Bio-Tech, University of Liège, Passage des déportés 2, 5030 Gembloux, Belgium. E-mail: francois.lehaire@ulg.ac.be*
Philippe LEJEUNE *Department of Forest and Nature Management, Gembloux Agro Bio-Tech, University of Liège, Passage des déportés 2, 5030 Gembloux, Belgium. E-mail: p.lejeune@ulg.ac.be*

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*Correspondence author.

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ABSTRACT

1. In recent decades, the wild boar *Sus scrofa* has simultaneously increased its population size and colonized new habitats, causing more ecological and socio-economic concern than perhaps any other ungulate species. However, the drivers and mechanisms of the species' spatial ecology remain poorly understood. Thanks to a recently developed framework, the movement ecology of any organism can now be tackled within a consistent and unified theoretical approach.
2. Based on this framework, we reviewed the literature on wild boar movement ecology to assess current knowledge and to identify important gaps.
3. By using important navigational (e.g. olfactory sense) and cognitive (e.g. spatial memory, learning from conspecifics) abilities, wild boar have developed complex movement strategies to cope with external factors. However, there is a lack of detailed information on the role played by the internal state (motivation) and motion capacity in shaping the spatial ability of the species.
4. Specific aspects of the movement ecology of the wild boar, together with its high diet plasticity and its high prolificacy, are probably the most important causes of the rapid spread of wild boar worldwide.
5. We hope our review will inspire other scientists to apply their biological models to the movement ecology paradigms. Furthermore, we suggest that future researchers dealing with the movement ecology of any species should explicitly state the components and interactions of the framework investigated to facilitate further understanding and comparison among studies.

INTRODUCTION

In recent decades, numbers of wild boar *Sus scrofa* have steadily been increasing (Apollonio & Andersen 2010). This increase has been accompanied by expansion in geographic range (Apollonio & Andersen 2010) and colonisation of new habitats, such as densely populated urban areas and landscapes dominated by agriculture (Cahill & Llimona 2004, Keuling et al. 2009, Podgórski et al. 2013). Recent studies on wild boar diet (Ballari & Barrios-García 2013), reproductive ability (Bieber & Ruf 2005, Gethoffer et al. 2007, Gamelon et al. 2013) and the interaction between these two factors (Bywater et al. 2010) have provided important insights into the causes of geographical expansion. However, the process that drives population spread, the movement of individuals, is often forgotten in the scientific literature. The socio-economic and ecological concerns generated by wild boar are such that this important element of the wild boar spread equation should be considered.

Movement decisions made by animals are the result of complex interactions between intrinsic and extrinsic factors and can have profound consequences for individual fitness, population dynamics and species distribution (Morales et al. 2010). Modern monitoring techniques (e.g. satellite telemetry) allow the collection of substantial numbers of high-resolution data on the spatial behaviour of animals. These kinds of data not only offer in-depth insights into movement patterns at different spatio-temporal scales, but also allow better understanding of the effect of physiological, demographic and ecological contexts on spatial behaviour.

A recently developed movement ecology framework (Nathan et al. 2008) provides a unified theory and an integrated approach for studying the spatial behaviour of any type of organism and offers a novel way to make use of the full potential of large datasets on movement. This conceptual framework (Fig. 1) defines movement as the result of the interplay between intrinsic factors (motivation/internal state, motion capacity, navigation capacity) and external factors (e.g. type of habitat, presence of a predator).

Knowledge of each of the components determining movement is important for many species, as it can greatly improve understanding of their spatial behaviour and how it is related to the environment. However, comprehensive reviews of the movement ecology of most species, including the wild boar, have not been carried out.

The aim of this paper is to summarise current knowledge of the drivers and mechanisms of the spatial behaviour of wild boar in relation to the movement ecology framework. For this, we made an exhaustive review of the current literature on movement ecology, based around the four components of the framework (motivation/internal state, motion capacity, navigation capacity and external factors) in relation to free-ranging wild boar, feral pigs (originating from feralization of the domestic pig), captive wild boar and domestic pigs *Sus scrofa* f. *domesticus*. Indeed, captive individuals demonstrate a return to behaviours observed in the wild soon after release (Boitani et al. 1992), and experimental studies on domestic animals provide a better understanding of the cognitive abilities of suids than studies of wild animals. Graves (1984) stated that the ‘study of wild and/or feral pigs provides insights into the behaviour of the domestic pig’; we make the inverse assumption, that the behavioural characteristics of domestic pigs reflect the behaviour of their wild ancestor. We did not

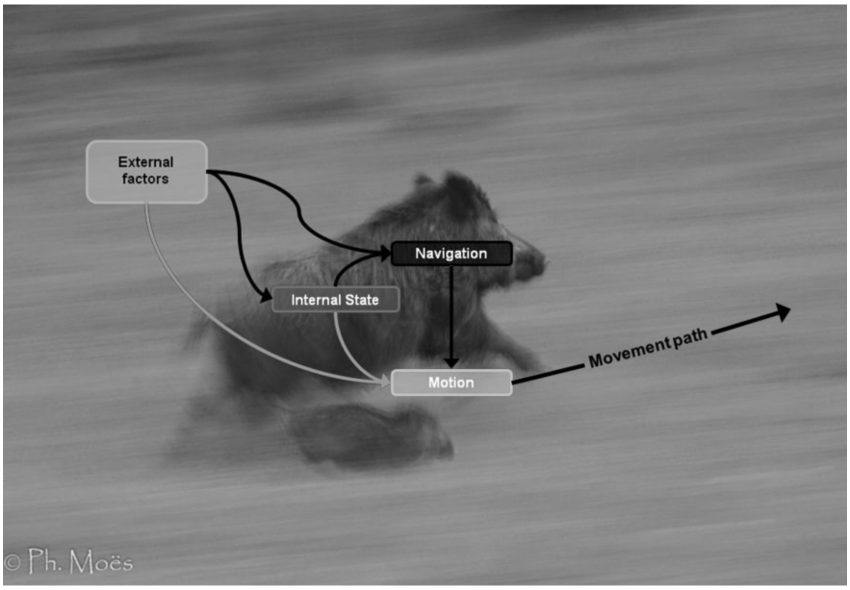

Fig. 1. The movement ecology framework, showing the four interacting components: motivation/internal state, motion capacity, navigation capacity and external factors. Adapted from Nathan et al. (2008).

consider studies on domestic pigs where the observed behaviour was attributed by the authors to the retention of the pigs in captivity.

INTERNAL STATE: WHY MOVE?

There are multiple internal motivations that drive exploration of the surrounding environment. Extrinsic exploration, with an acute need driven by physiological state (e.g. to gain energy, escape predators or reproduce), and intrinsic exploration, driven by cognitive abilities (e.g. scanning the environment, assessing resources), are two key components of movement decisions (Studnitz et al. 2007).

Energy gain and expenditure

The search for food is the mechanism by which mobile organisms fulfil energetic requirements, and it is one of the main drivers of the movement of ungulates (Leblond et al. 2010, Wilson et al. 2012). Depending on resource abundance, quality and distribution, wild boar are active for 40% to 65% of their time, either foraging or travelling (Graves 1984, Cousse & Janeau 1992, Russo et al. 1997), so their energetic requirements are important. Wild boar are highly adaptable and can quickly change their movement behaviour in response to environmental conditions (Podgórski et al. 2013), giving them the ability to adjust foraging behaviour and balance their energetic yields. When environmental conditions change or when energy demands increase, they employ an anti-starvation strategy: they intensify visits to sites where food with higher energetic value is available (Held et al. 2005) and increase their movement rate within their home range to fulfil their needs (Singer et al. 1981, Massei et al. 1997). Studies on foraging strategies have shown that crossbred pigs (one domestic parent and one wild parent) employ a costlier 'win–shift' strategy, moving between patches more frequently, compared with domestic pigs, which adopt a 'win–stay' strategy (Gustafsson et al. 1999). This difference in behaviour can be explained by the adaptation of wild animals to cope with predation risk (Tolon et al. 2009) and conspecific competition (Újváry et al. 2012), an adaptation that is redundant in captivity.

Reproduction

The spatial behaviour of males and females differs, largely due to differences in energetic requirements (Harestad & Bunnell 1979, Saunders & McLeod 1999), mating strategies (Clutton-Brock 1989) and parental behaviour (D'Eath & Turner 2009). Adult males and females rarely interact outside of the reproductive period. During the mating season, interactions are more frequent, and adult males temporarily join groups of females (Dardaillon 1988). After giving birth, females restrict their movement to a small area around the farrowing site and are isolated from their social groups for 1–2 weeks (Mauget 1983). During this period, females move less and show a high degree of fidelity (D'Eath & Turner 2009) to a limited number of resting sites surrounded by habitats that maximize safety and resource availability, thus helping to ensure the successful rearing of the litter (Janeau et al. 1995). However, lactation increases a female's energetic needs, so more time is devoted to foraging activities (Russo et al. 1997). The movement range of females gradually increases with the age of their piglets (Spitz 1992).

Learning

Experience gained from the environment and from conspecifics plays a major role in the development of the spatial memory and social behaviour of wild boar (Spitz & Janeau 1995). Domestic pigs exhibit cooperative behaviour and learn conditioning tasks rapidly (D'Eath & Turner 2009), and social reinforcement is an important incentive to complete spatial tasks (Laughlin & Mendl 2000, Mendl et al. 2010). Through social interactions, piglets learn what food resources can be acquired as well as where and when to find them (Nicol & Pope 1994). This is confirmed by observations in the wild of similar spatial behaviours adopted by individuals in groups (Zaĭtsev 1996).

Personality

Individual behavioural variations can lead to different spatial abilities and perceptions of the surrounding environment. Back-test experiments on piglets (i.e. placing the animal in the supine position and quantifying the amount of time spent struggling and the number of struggle attempts) can be used to assess personality in the early stages of life (Hessing et al. 1993). Proactive individuals showing active responses to the back-test tend to develop dominance and out-competing behaviour. Relying on previous experience and developing behaviour based on routines, they are well adapted to stable environments. Reactive individuals showing passive responses to the test rely more on environmental stimuli and demonstrate a better ability to cope with environmental changes (Coppens et al. 2010). Differences in explorative behaviour tested in release experiments show that some individuals adopt constant and progressive explorative behaviour, while others prefer to explore a whole area extensively before starting detailed exploration and beginning to utilise particular areas (Boitani et al. 1992). Personality is also demonstrated in the wild by individuals expressing various spatial strategies within the same study areas (Keuling et al. 2008a) and from year to year (Keuling et al. 2009).

MOTION CAPACITY: HOW TO MOVE?

Motion capacity is the overall ability to move, which encompasses factors such as speed (slow, medium, fast), mode (intermittent, steady state, acceleration, deceleration) and substrate (surface, slope, compliance, obstacles), and the results of evolutionary pressures such as the need for food acquisition, predation avoidance and social interactions (Reilly et al. 2007).

Mechanically and functionally, like all artiodactyls, wild boar transverse-gallop by moving diagonal legs forward at the same time (Jansen et al. 2009). In their evolution, Suidae have maintained an unguligrade foot posture, but they lack the elongated distal segments present in other living unguligrades (e.g. deer, pronghorn) that are necessary for fast running for extended periods (Clifford 2010). Wild boar are thus not generally regarded as fast runners, although they can run fast for a few minutes. They compensate for their short step size – 20–25 cm for piglets and up to 45 cm for adults – by adopting a high step frequency (Briedermann 1990). Compared with the digitigrade foot posture, unguligrady allows animals to take a longer movement step, thus reducing the per-distance cost of locomotion. Consequently, wild boar unguligrady is an adaptation providing an energetic advantage at lower speeds, rather than an adaptation for fast running (Briedermann 1990).

Wild boar can move at different speeds depending on the situation. Movements slower than 1 km/h are used for feeding, exploring, wallowing and marking, while fast movements, such as trotting and galloping, are associated with excursions and escape behaviours (Mainland et al. 2007). When trotting, wild boar can reach speeds of 6–10 km/h. This mode is used during social contact (e.g. by juveniles playing) and for inter-patch movement. When galloping, mostly in fleeing circumstances, wild boar can reach speeds of 10–40 km/h (personal observation). This relatively low speed compared with that of other animals of similar size (Garland 1983) could be the result of an evolutionary predator–prey arms race in which selection pressure generated by chasing predators is rather low: wolves, the only significant predator of wild boar, cause less than 20% of natural mortality (Jędrzejewska & Jędrzejewski 1998, Wagner et al. 2012). Adult wild boar can defend themselves against predators and are rarely attacked by wolves, which predominantly target young cohorts (Jędrzejewski et al. 2000, Wagner et al. 2012).

Wild boar are able to employ different movement strategies. Daily, they exhibit three clear patterns of movement (Spitz & Janeau 1990). The staying strategy consists of remaining within a limited area, the activity zone, and moving short distances at different speeds. This strategy is mostly used by females accompanied by piglets, for activities such as resting or social interaction. The ranging strategy, usually employed by males at night, consists of ranging outside the activity zone. The third strategy, any combination of the two first strategies, results in complex movement paths, e.g. looping or zigzag patterns.

Daily movements that are longer than the home range radii are commonly observed (Spitz & Janeau 1990), and daily ranges often cover large parts of wild boars' entire annual range. The annual home range size of wild boar is thus quite small considering the movement ability of the species, and they are able to move over their entire seasonal range within a 24-hour period, confirming their generally sedentary behaviour. Podgórski et al. (2013) showed that the daily range covered by wild boar was 1.3 km^2 in a natural environment, corresponding to 45% of the annual range, and 2.4 km^2 in urban areas, corresponding to 90% of the annual range. The mean daily distances travelled were estimated to be 7.2 km in a natural environment and 11.4 km in urban areas. In agro-forested landscapes, Keuling et al. (unpublished data) found a daily moved distance ranging in average between 3 and 4 km and reaching a maximum of 12 km. The duration of wild boar activity ranges from 6.8 hours/day in natural habitats through 7.2 hours/day in agro-forested environments to 12.9 hours/day in peri-urban areas (Spitz & Janeau 1990).

Wild boar have good swimming and jumping capacities (Briedermann 1990). Observations of wild boar swimming across large rivers and off coastlines are common, and they have also been seen to make long jumps and jumps of up to 1.20 m in height (Hammell et al. 1975).

NAVIGATION CAPACITY: WHERE AND WHEN TO MOVE?

Understanding an animal's navigational capacity requires information about its perceptual, sensory and cognitive abilities. Navigational capacity is often associated with targets (e.g. food items, refuges, mates) and cues that individuals are able to use (Nathan et al. 2008). Two sorts of cues, allothetic or ambient cues and idiothetic or self-movement cues, drive animals' orientation in space and define the movement strategies employed (Whishaw et al. 2001).

By using ambient cues (e.g. sights, sounds, smells and the Earth's magnetic field), animals can create a spatial map of the environment and move with a strategy called piloting (Whishaw et al. 2001). In wild boar, olfaction is the most developed sense and plays an important role in navigation, foraging, social interactions and vigilance (Briedermann 1990). According to Lemel et al. (2003), the olfactory ability of wild boar is more effective under humid than dry air conditions, which could explain why they are more active when the relative air humidity is higher. Piglets use olfaction to find their way back to the nest or family group in the early stages of life (Kittawornrat & Zimmerman 2011).

Olfaction plays a major role in searching for food at small spatial (metre) scales (Suselbeek et al. 2012) and in detecting the potential presence of predators (Kuijper et al. 2014). In dense forest habitat, the assessment of predation risk by wild boar seems to be more dependent on the use of olfactory cues than on habitat visibility (Kuijper et al. 2014). The visual acuity of pigs is indeed poorly developed (Zonderland et al. 2008) compared with olfaction (Croney et al. 2003). When assessing environmental factors, pigs can barely discriminate by using vision (Lomas et al. 1998) and are also poor at discriminating colours (Jankevicius & Widowski 2004). However, they do seem able to rely on their vision to collect information on what is immediately in front of them, which could explain their use of directed movement in fleeing circumstances (Tolon et al. 2009). The auditory capacity of wild boar covers a spectrum from 42 to 40500 Hz and is mainly used in social interactions (Briedermann 1990).

By means of idiothetic cues, animals can use information directly recorded from their own movement (e.g. speed, distance and direction) via their vestibular system, muscle and joint receptors, or optic flow (Whishaw et al. 2001). Animals use these cues in a strategy called dead reckoning, path integration or route-based navigation, which is based on the assumption that animals are able to estimate the direction of their movement by using the position of the sun or stars or the Earth's magnetic field. It can be used by an animal to find its way back to familiar areas, such as resting or feeding places, within the home range (Etienne et al. 1996). In an experiment in which they had to find a hidden bowl of food, pigs demonstrated an awareness of their own actions and movement ability that may demonstrate a dead reckoning strategy (Broom et al. 2009).

Global cues

Magnetic cues have been shown to influence the body orientation of resting and grazing ungulates (Begall et al. 2008), including wild boar (Červený et al. 2012). Wild boar seem to display magnetic alignment by preferentially orienting their body in a NNE–SSW direction, facing NNE. Resting pairs seem to adopt an anti-predation strategy by positioning themselves facing in opposite directions (Červený et al. 2012). Observations of synchronized behaviour between individuals in a group, such as parallel body orientation, confirm this (Zaĭtsev 1996). However, how the magnetic field is used for navigation in the landscape remains unclear and requires further investigation.

Spatial memory

Suids are able to solve complex spatial memory tasks, e.g. by remembering the locations of foods of different values (Held et al. 2005) and utilizing previous experiences (Mendl et al. 1997, Laughlin & Mendl 2000), highlighting the use of memory rather than food-related cues in systematic searches (Mendl et al. 1997, Suselbeek et al. 2012). In the wild also, regular re-use of the same resting areas suggests the use of memory by wild boar for navigation (Spitz & Janeau 1990). In relocation trials, wild boar found food in fewer visits than would be expected by chance, indicating that they could remember locations of food. In the wild, foraging activities, e.g. grassland rooting (Bueno et al. 2009), mainly occur in the vicinity of resting sites, through exploration of the environment or by re-visiting of known profitable food sites (Spitz & Janeau 1995). Wild boar do not select resting places and activity zones randomly, but rather by means of directed or memory-based movement between familiar environments (Spitz & Janeau 1990). Remembered landmarks in the environment seem to allow wild boar to create internal maps or route systems (Dardaillon & Beugnon 1987). They also use scent marks to navigate within their home range (Bracke 2011). Memory-based mechanisms may also facilitate escape movements via routes known through previous experience (Tolon et al. 2009).

EXTERNAL FACTORS

Resources

The distribution and abundance of resources greatly affect movement patterns. The homogeneous distribution of high-quality and abundant food, water and shelter on a small spatial scale usually leads to a small home range. When supplementary food is provided, artificially increasing the quality of the habitat, wild boar can modify their spatial behaviour around baiting areas, which leads to smaller home range sizes (Keuling et al. 2008a). In a rich habitat that provides easy access to food all year and safe resting sites, wild boar restrict their movement to a smaller area and thus reduce energy expenditure (Massei et al. 1997), in accordance with the food-exploitation hypothesis. In poor nutritional conditions, wild boar move more in search of food and water, consequently increasing their home range (Caley 1997, Massei et al. 1997); however, when animals are near starvation, saving energy becomes the priority, and home ranges thus become very small. The effect of food abundance on home range size is widely debated: some research suggests that home ranges are smaller when food is easily available (Singer et al. 1981, Boitani et al. 1994), some that they are smaller under poor natural conditions (Caley 1997, Massei et al. 1997). Wild boar activity is more evenly spread throughout the day in natural habitats than in human-dominated landscapes (Podgórski et al. 2013). In these peri-urban environments, depending on the resource distribution, wild boar can exhibit contrasted spatial behaviour, either restricting (Dinter 1991) or increasing (Podgórski et al. 2013) displacement between focal foraging areas. Density-dependent effects of resources also strongly affect wild boar spatial behaviour. The density-dependent hypothesis predicts smaller home ranges (Massei et al. 1997) and increased activity (Andrzejewski & Jezierski 1978) when population size increases. Bertolotto (2010) related this hypothesis to food availability, showing that when population density is high and food availability low, competition increases, and wild boar increase their movement rate to search and compete for food. In contrast, when population density is low and food availability high, there is less competition and movement because wild boar can find high-quality resources in their immediate surroundings.

Seasonality of resources

Wild boar can adapt to the seasonality of food resources by adjusting spatial behaviour accordingly, e.g. by reducing movement and home range in areas rich in masting trees in autumn (Kurz & Marchiton 1972, Singer et al. 1981, Bertolotto 2010). In summer, cultivated crops provide highly attractive food and shelter for wild boar, and migrations towards cultivated lands are observed (Cargnelutti et al. 1990, Keuling et al. 2009). Range shifts or seasonal dislocations have been observed under various environmental conditions (Singer et al. 1981, Keuling et al. 2009), highlighting the plasticity of the species. The distance moved during habitat shifts varies between individuals (Gerard et al. 1991) and depends on the distance from the resting site to the crop fields. Animals located more than 2 km from the cropland remain in the forest at night (Singer et al. 1981). Seasonal dislocations can also have climatic drivers. In mountains, wild boar tend to shift their ranges towards lower elevations in summer synchronically with mast production (Singer et al. 1981). Inter-annual and unpredictable variations in resource availability can play an important role in shaping wild boar movement patterns. For example, in Mediterranean areas drought can temporally limit water availability, and consequently, wild boar move closer to ditches as water levels in them decrease (Bertolotto 2010).

Conspecifics

Social interactions are important in shaping wild boar movement (Cousse et al. 1994). Females forming social groups tend to show similar spatial behaviour (Boitani et al. 1994, Keuling et al. 2008a, 2009). Their close movement association is stronger during the day, e.g. in the choice of resting sites, and weaker at night and in poor-quality habitats (Hebeisen 2007). Access to food resources within wild boar groups, as in many foraging groups of social mammals, seems to be achieved by means of a scrounger–producer interaction between foraging individuals (Giraldeau & Caraco 2000). In this strategy, a dominant individual, the scrounger, obtains information about the location of lucrative feeding sites from its group mates, the producers (Krosniunas 1979). Using this strategy, the dominant individual limits its energy expenditure in searching for food (Giraldeau & Caraco 2000).

Predator avoidance

Within its current geographic range, mortality of the wild boar from wild predators is outweighed by mortality from hunting (Toïgo et al. 2008, Keuling et al. 2013). The species exhibits natural and hunting-induced anti-predatory strategies which affect movement patterns. If disturbed (e.g. by hunting), wild boar try to reduce the distance they move between resting sites to limit predation risk (Fernández-Llario 2004). However, if resting sites are scarce, searching for refuges can lead to an enlargement or shift in the home range (Sodeikat & Pohlmeyer 2007). The shift can be related to the duration of the hunting season and is directed towards refuge areas, mainly within forests and crop fields, which provide both cover and food resources to avoid competition (Thurfjell et al. 2013). Disturbance has a great effect on the daily distances travelled and habitat selection patterns of females (Janeau et al. 1995), which may lead to increased sexual segregation during high-risk periods (Saïd et al. 2012).

The spatial behaviour of wild boar changes according to the varying intensity of hunting pressure. Fleeing behaviour is common where hunting pressure is high; hiding behaviour is more common where hunting pressure is low (Thurfjell et al. 2013). Driven hunts may increase the mean area of the resting range (Sodeikat & Pohlmeyer 2007) and cause temporary emigration from the home range (Sodeikat & Pohlmeyer 2003), while single hunts, i.e. individual hunters stalking or shooting from hides at baiting stations or at the edges of fields, may reduce movement (Tolon et al. 2009, Thurfjell et al. 2013) and home range size (Keuling et al. 2008b). Apart from a shift in daytime resting sites to locations farther away from hunting sites, Keuling et al. (2008b) found no clear differences between the effects of driven hunts and single hunts on the spatial behaviour of wild boar. However, Thurfjell et al. (2013) found that when hunting takes place but wild boar are not the target, as well as when still hunting (waiting for game) is used, individuals react by lowering their activity and adopting hiding behaviour. Lower hunting pressure favours diurnal activity patterns (Keuling et al. 2008b) and movement inside the usual range (Scillitani et al. 2010). Thus, disturbance created by hunting only seems to affect wild boar on a small spatial scale; this is confirmed by the more limited daily movements of wild boar after hunting (Singer et al. 1981).

Weather conditions

Adverse weather, such as snow and drought, affects the movement patterns of wild boar (D'Andrea et al. 1995) by reducing their movements (Thurfjell et al. 2014). Activity levels and distances moved decrease as the temperature drops (Briedermann 1971, 1990, Massei et al. 1997, Keuling et al. 2008a). In captive wild boar, activity decreases with temperature (Blasetti et al. 1988). When the temperature drops below −5 °C and there is snow, wild boar use more directed foraging searches (Lemel et al. 2003) in order to reduce periods of activity by 1.5 hours per day and save energy (Truve 2004). Snow is supposed to be a limiting dispersal factor for the geographic expansion of wild boar (Erkinaro et al. 1982, Rosvold & Andersen 2008) and may restrict local movements (Lemel et al. 2003).

In hot and dry air conditions, wild boar, physiologically constrained by their lack of a thermoregulation system, search for shade, water and cool moist forest areas (Howe et al. 1981, Dexter 1998). When the constraint of high temperatures decreases, food availability again becomes the central factor driving wild boar distribution (Dexter 1998). Windy conditions can also affect the movement of wild boar by reducing their activity (Lemel et al. 2003, Truve 2004).

Landscape structure

Landscape features such as crop fields, hedges and ditches (Thurfjell et al. 2009), riparian corridors (Caley 1997), ridges offering protective cover (Gérard et al. 1992) and forest corridors favour the movement of wild boar over long distances, allowing exchange between populations and range expansion (Garcia et al. 2011). In contrast, human infrastructures such as highways can reduce rates of diurnal movement (Corlatti et al. 2009). However, wild boar do cross bridges, motorways, adapted culverts and overpasses, which demonstrates the ability of the species to cope with human infrastructure (Mata et al. 2008). Local movement can also be restricted by fences along roads and cropland areas (Hone & Atkinson 1983, Massei et al. 1997). On farmland, electrification of fences lowers intrusion into crop fields by 65% (Reidy et al. 2008). In an experimental trial, Hone & Atkinson (1983) showed that only 6.3% of pigs cross electric fences.

Human-induced movement

The current distribution of wild boar originates in part from post-glacial natural expansion (Alexandri et al. 2012), but the role of humans is significant. Historically, agricultural development and the domestication of wild pigs played a role in large-scale movements (Larson et al. 2005), and human-mediated gene flow has occurred in the European population of wild pigs (Scandura et al. 2008). More recently there have been local reintroductions, illegal releases and individual escapees from farms (Goulding 2001). Illegal translocations are usually undertaken by hunters to supplement recreational hunting stock and can allow the species to make large jumps in its geographical range, from 50 to 400 km (Spencer & Hampton 2005). Truvé et al. (2004) found that the wild boar population expansion velocity in Sweden (4.8 km/year) was higher than expected (3.0 km/year), which could be explained both by an underestimation of long-distance dispersers and by introduced populations.

DISCUSSION AND CONCLUSIONS

We have shown the importance of navigational and cognitive abilities (e.g. spatial memory, learning from conspecifics) in shaping the spatial behaviour of wild boar and in enabling them to develop complex movement strategies. Table 1 synthesises most of the current knowledge concerning the four components of the movement ecology framework. In summing up what is known about wild boar spatial behaviour, we also exposed existing knowledge gaps, such as the lack of information in the literature about the role played by internal state and motion capacity in shaping the spatial ability of the species. Table 2 synthesises the gaps in the literature on wild boar movement ecology and gives examples of studies dealing with these missing components.

Integrating the internal state of the animal into studies would allow researchers to consider inter-specific variability, recently shown to be an important parameter in behavioural ecology (Roshier et al. 2008), and occurring in wild boar, as illustrated in this review. Quantifying individual variability in movement behaviour is a prerequisite to understanding the emergence of population-scale patterns (Singh et al. 2012). However, in free-ranging populations, it is easier to study the influence of extrinsic than intrinsic stimuli (e.g. physiological states or cognitive processes, genetic traits, sensory acuteness) on spatial behaviour. Wild boar can adapt their spatial strategies, e.g. by reducing or increasing their home range size depending on the external environment, the weather or food availability, but it is unknown exactly how their internal state triggers their decision to move. Obtaining relevant information on the physiological state of the individual, such as the heart rate, temperature or stress level, is now possible thanks to a new generation of tracking devices (Jachowski et al. 2013).

When considering the motion capacity of wild boar, integrating the energetic cost of locomotion into research may

Table 1. Synthesis of current knowledge on wild boar *Sus scrofa* movement ecology, organised around the four components of the movement ecology framework (Nathan et al. 2008)

Component		Effect on movement	Animal	Representative references
Internal state				
Energetic balance	Food intake at the patch level	Win–shift strategy: increased movement between patch resources	Domestic and crossbred pigs	Laughlin and Mendl (2000)
	Social foraging	Scrounger–producer strategy: decreased movement for dominant individual	Feral boar	Krosniunas (1979)
Safety	Large spatio-temporal scale	Complete home range shift during hunting season to hunting-free area	Wild boar	Tolon et al. (2009)
	Small spatio-temporal scale	Hiding and fleeing behaviour only in direct contact with disturbance	Wild boar	Maillard and Fournier (1995)
Reproduction	Female	Decreased movement during parturition and weaning	Wild boar	Janeau et al. (1995)
	Male	Increased movement during mating season	Wild boar	Singer et al. (1981)
Learning	From birth to maturity	Development of memory and social behaviour during growth	Wild boar	Singer et al. (1981)
		Learning to cope with environmental changes; e.g. seasonal altitudinal migration	Domestic pigs	Mendl et al. (2010)
Sex	Male	Move more than females	Wild boar	Caley (1997)
		Have generally larger home range than females	Wild boar	Singer et al. (1981)
	Female	Spend more time on slow movement	Wild boar	Spitz and Janeau (1995)
Age	From birth to maturity	Movement similar for individuals of the sounder (social unit organised around 2–3 adult females and their most recent litters)	Wild boar	Cousse and Janeau (1992)
	At maturity	Dispersal	Wild boar	Truve and Lemel (2003)
Personality	Temperament, from back-test	Proactive individuals move more and develop routine in stable environment	Domestic pigs	Coppens et al. (2010)*
		Reactive individuals move less and cope better with environmental changes		
	In the wild	Dominance, aggression and increased movement	Wild boar	Singer et al. (1981)
Motion capacity				
Locomotion mode		Unguligrady provides energetic benefits at low speed	Wild boar	Briedermann (1990)
		Ability to switch from slow to fast locomotion mode	Wild boar, domestic pigs	Mainland et al. (2007)
Navigation capacity				
Ambient cues	Olfactory	Important role in navigation, foraging, social interactions and avoidance of predators	Wild boar	Briedermann (1990)
		Acts at small scale (metres)	Wild boar	Suselbeek et al. (2012)
	Vision	Poorly developed but efficient for directed movement (e.g. fleeing)	Wild boar Domestic pigs	Tolon et al. (2009) Zonderland et al. (2008)
	Sounds	Well developed, mostly used for social interactions	Wild boar	Briedermann (1990)
Self-movement cues		Evidence of awareness of own movement	Domestic pigs	Broom et al. (2009)
Global cues		Resting individuals display magnetic alignment. Potential role in movement not yet understood	Wild boar	Červený et al. (2012)
Spatial memory	Landmarks	Ability to memorize environmental features (relief, flora, soil)	Wild boar	Lozan (1995)
		Use of internal maps, route-navigation	Wild boar	Dardaillon and Beugnon (1987)
	Scent marks	Use of scent marks to navigate within the home range	Wild and feral boar, domestic pigs	Bracke (2011)*
External factors				
Local resources	Habitat quality	Increased movement in poor quality habitat, decreased movement in rich habitats	Wild boar	Russo et al. (1997)
	Water	Riparian areas favour extensive movement	Wild boar	Caley (1997)

Table 1. (*Continued*)

Component		Effect on movement	Animal	Representative references
Ephemeral resources	Water	In dry areas, movement restricted to water resources	Wild boar	Bertolotto (2010)
	Acorns	Increased movement in poor crop conditions	Wild boar	Singer et al. (1981)
Seasonal resources	Crops	Seasonal movement between low/high elevation	Wild boar	Singer et al. (1981)
		Seasonal migrations to cropland when present	Wild boar	Dardaillon (1987)
Predators	Hunting pressure	If pressure low: increased movement within the home range If pressure high: excursions outside the home range	Wild boar	Keuling et al. (2008b)
	Hunting method	Hunting with dogs increases distance between resting sites	Wild boar	Maillard and Fournier (1995)
Conspecifics		High density results in increased long distance (>10 km) dispersal	Wild boar	Cargnelutti et al. (1992)
Weather conditions	Temperature	Decreased movement at low temperatures	Wild boar	Singer et al. (1981)
	Relative air humidity	Increased activity in humid air conditions	Wild boar	Lemel et al. (2003)
	Snow	Snow cover limits movement at local and regional scale	Wild boar	Lemel et al. (2003) Rosvold and Andersen (2008)
Barriers	Road infrastructure	Limits movement partially but does not affect gene flow	Wild boar	Frantz et al. (2012)
		Can be a barrier for dispersal	Wild boar	Jerina et al. (2005)
	Mountains	Movement occurs along mountain ridges	Wild boar	Jerina et al. (2005)
	Protection fences	Prevent local movement	Feral boar	Reidy et al. (2008)
Period of the day		Increased movement around dawn and dusk	Wild boar	Caley (1997)

*Review.

provide interesting insights into constraints and benefits associated with movement (Nishii 2006). Studies on gait, mechanics and limb kinematics could complete our understanding of time and energy budgets, and observation of skeletal adaptations might highlight differences between wild boar populations from forests, plains and peri-urban areas (Reilly et al. 2007).

Information on acceleration on the x, y and z axes has been made available by the new generation of satellite telemetry collars. This information could help us understand motivation for movements and behavioural responses to various intrinsic and extrinsic stimuli (Löttker et al. 2009). However, disentangling behaviour (e.g. lying down, standing, foraging, walking, loping, galloping)

Table 2. Identified knowledge gaps in the four components of wild boar movement ecology

Component	Gap	Available method	Data requirement	Example of studies from other species
Internal state	Physiological state	Bio-loggers	Energetics, stress levels	Jachowski et al. (2013)
Motion capacity	Defining behaviour associated with movement	Satellite tags with accelerometers	Acceleration data	Brown et al. (2012)
	Energetic cost of displacement in contrasting environmental conditions		Locomotion parameters, e.g. stride period/length, leg trajectory	Nishii (2006)
Navigation capacity	Perception range	Fractal analysis	Experimental design and movement patterns analysis	With (1994)
	Disentangling cues used: memory, landmarks	Translocation, environmental change, ontogenic tracking	Movement patterns analysis, long-term tracking data	Fagan et al. (2013)
	Drivers of dispersal timing: when to start and where to stop	Ontogenic tracking	Environmental and satellite tracking data at fine spatio-temporal scale	Clobert et al. (2012)
External factors	Intra-specific and inter-specific interactions	Satellite tags, proximity loggers		Böhm et al. (2009)

from accelerometer sensor data is still in its infancy and requires further testing and assessment with the help of controlled experiments (Wevers et al. 2011).

Though use of cues seems to play an important role in creating an internal map of the environment, e.g. by identifying locations of resource patches, predation risk or conspecifics, many questions about the navigational and cognitive abilities of the species remain. The perceptual range over which wild boar are able to sense environmental cues is still poorly known, and this lack of knowledge has many management implications (e.g. in agricultural practices, baiting and hunting strategies).

Studying the role of spatial memory has so far only been possible in controlled experiments with captive or domestic individuals. With precise information on movement paths from satellite tracking data, it is now possible to tackle this issue with wild individuals. Various methods are used to assess the role of memory in animal movement: translocation of individuals into an unknown environment, modification of resources or barriers to movement within the landscape, and ontogenic tracking (monitoring of juveniles during their different developmental stages; Fagan et al. 2013). Experiments could be used to determine how wild boar use memory, though landscape feature modification and translocation may be difficult to implement directly in the field. Displacement of individuals causing problems, e.g. in peri-urban areas where shooting is prohibited, may offer an opportunity to observe reactions in a novel environment. Using satellite data, analysis of return points or the recursion distribution by means of Fourier or wavelet analysis (Riotte-Lambert et al. 2013) may clarify how individuals use memory. For example, loop movements from resting sites in wild boar suggest a central place foraging strategy that requires either path integration or a mind map of resting areas and nearby foraging areas.

Knowing what environmental and internal conditions make an animal move and establish a new home range is important for understanding processes occurring at the population scale, such as the expansion of the geographical range. More specifically, precise remote tracking of dispersing individuals could provide information about (i) the influence of the environment on the path followed, (ii) the reasons a final location is selected for establishment, (iii) the cues that are used when dispersing and (iv) the functional connectivity of the landscape. Following individuals from their birth could provide information about the complete historical movements of an individual and the development of memory-enhanced movement abilities and patterns. From a behavioural and locomotion perspective, this would help explain exactly what happens when an individual decides to disperse.

Studying the movement tracks of individuals within a subset of the species' range can provide only limited information (Avgar et al. 2013). Analysis of animal movement abilities within different landscape configurations and compositions is required for a complete understanding and to provide reliable predictive models on which management recommendations can be based. In this framework, building a spatial database, taking EURODEER (Urbano et al. 2010) as an example, may offer opportunities for large-scale analysis and comparison of movement tracks of wild boar under various environmental conditions and geographical areas, giving a better understanding of their movement ecology.

Animal movement cannot be comprehensively explained by internal state, by motion and navigation capacities or by external factors considered solely. Rather, the interaction of all components needs to be taken into account for a thorough understanding of observed movement paths. Such interactions can be incorporated into individual-based models simulating movement in a range of physiological and behavioural states, as well as environmental conditions (Patterson et al. 2008). Since many parameters of the four components are not yet readily available for modelling, it is necessary to use approximations to inform the models, but an influx of data in the near future will enable model verification and realistic predictions. For this reason, we emphasize the need for models on wild boar movement that incorporate all the different components of movement ecology.

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REFERENCES

Alexandri P, Triantafyllidis A, Papakostas S, Chatzinikos E, Platis P, Papageorgiou N, Larson G, Abatzopoulos TJ, Triantaphyllidis C (2012) The Balkans and the colonization of Europe: the post-glacial range expansion of the wild boar, *Sus scrofa*. *Journal of Biogeography* 39: 713–723.

Andrzejewski R, Jezierski W (1978) Management of a wild boar population and its effect on commercial land. *Acta Theriologica* 23: 309–339.

Apollonio M, Andersen R (2010) *European Ungulates and Their Management in the 21st Century*. Cambridge University Press, Cambridge, UK.

Avgar T, Mosser A, Brown GS, Fryxell JM (2013) Environmental and individual drivers of animal movement patterns across a wide geographical gradient. *Journal of Animal Ecology* 82: 96–106.

Ballari SA, Barrios-García MN (2013) A review of wild boar *Sus scrofa* diet and factors affecting food selection in native and introduced ranges. *Mammal Review* 44: 124–134.

Begall S, Červený J, Neef J, Vojtčch O, Burda H (2008) Magnetic alignment in grazing and resting cattle and deer. *Proceedings of the National Academy of Sciences of the United States of America* 105: 13451–13455. doi:10.1073/pnas.0803650105.

Bertolotto E (2010) *Behavioural Ecology of Wild Boar* (Sus scrofa) *in an Apennine Environment*. PhD thesis, University of Sassari, Sassari, Italy.

Bieber C, Ruf T (2005) Population dynamics in wild boar *Sus scrofa*: ecology, elasticity of growth rate and implications for the management of pulsed resource consumers. *Journal of Applied Ecology* 42: 1203–1213.

Blasetti A, Boitani L, Riviello MC, Visalberghi E (1988) Activity budgets and use of enclosed space by wild boars (*Sus scrofa*) in captivity. *Zoo Biology* 7: 69–79.

Boitani L, Mattei L, Morini P, Zagarese B (1992) Experimental release of captivity reared wild boar (*Sus scrofa*). In: Spitz F, Janeau G, Gonzales G, Aulagnier S (eds) *Proceedings of the 'Ongulés/Ungulates 91' International Symposium*, 413–417. Société Francaise pour l'Etude et la Protection des Mammifères, Paris, and Institut de Recherche sur les Grands Mammifères, Toulouse, France.

Boitani L, Mattei L, Nonis D, Corsi F (1994) Spatial and activity patterns of wild boars in Tuscany, Italy. *Journal of Mammalogy* 75: 600–612.

Böhm M, Hutchings MR, White PCL (2009) Contact networks in a wildlife–livestock host community: identifying high-risk individuals in the transmission of bovine TB among badgers and cattle. *PLoS ONE* 4: e5016. doi:10.1371/journal.pone.0005016.

Bracke MBM (2011) Review of wallowing in pigs: description of the behaviour and its motivational basis. *Applied Animal Behaviour Science* 132: 1–13.

Briedermann L (1971) Zur Reproduktion des Schwarzwild in der Deutschen Demokratischen Republik. *Beiträge zur Jagd und Wildforschung* 7: 169–186.

Briedermann L (1990) *Schwarzwild*. VEB Deutscher Landwirtschaftsverlag, Berlin, Germany.

Broom DM, Sena H, Moynihan L (2009) Pigs learn what a mirror image represents and use it to obtain information. *Animal Behaviour* 78: 1037–1041.

Brown DD, LaPoint S, Kays R, Heidrich W, Kümmeth F, Wikelski M (2012) Accelerometer-informed GPS telemetry: reducing the trade-off between resolution and longevity. *Wildlife Society Bulletin* 36: 139–146.

Bueno CG, Alados CL, Gomez-Garcıa D, Barrio IC, Garcıa-Gonzalez R (2009) Understanding the main factors in the extent and distribution of wild boar rooting on alpine grasslands. *Journal of Zoology* 279: 195–202.

Bywater KA, Apollonio M, Cappai N, Stephens PA (2010) Litter size and latitude in a large mammal: the wild boar *Sus scrofa*. *Mammal Review* 40: 212–220.

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

Caley P (1997) Movements, activity patterns and habitat use of feral pigs (*Sus scrofa*) in a tropical habitat. *Wildlife Research* 24: 77–87.

Cargnelutti B, Gerard J-F, Sptiz F, Valet G, Sardin T (1990) Occupation par le sanglier (*Sus scrofa*) des habitats d'un agro-écosystème modifié lors de la mécanisation de l'agriculture. *Gibier, Faune Sauvage* 7: 53–66.

Cargnelutti B, Spitz F, Valet G (1992) Analysis of dispersion of wild boar (*Sus scrofa*) in Southern France. In: Spitz F, Janeau G, Gonzales G, Aulagnier S (eds) *Proceedings of the 'Ongulés/Ungulates 91' International Symposium*, 423–425. Société Francaise pour l'Etude et la Protection des Mammifères, Paris, and Institut de Recherche sur les Grands Mammifères, Toulouse, France.

Červený J, Burda H, Ježek M, Kušta T, Begall S (2012) Magnetic alignment in wild boars. In: Keuling O (ed) *9th International Symposium on Wild Boar and Other Suids*. 4. Institute for Terrestrial and Aquatic Wildlife Research, University of Veterinary Medicine, Hannover, Germany.

Clifford AB (2010) *Evolution and Mechanics of Unguligrady in Artiodactyls*. PhD thesis, Brown University, Providence, Rhode Island, USA.

Clobert J, Baguette M, Benton TG, Bullock JM (2012) *Dispersal Ecology and Evolution*. Oxford University Press, Oxford, UK.

Clutton-Brock TH (1989) Mammalian mating systems. *Proceedings of the Royal Society Biological Sciences Series B* 236: 339–372.

Coppens CM, de Boer SF, Koolhaas JM (2010) Coping styles and behavioural flexibility: towards underlying mechanisms. *Proceedings of the Royal Society Biological Sciences Series B* 365: 4021–4028.

Corlatti L, Hackländer K, Frey-Roos F (2009) Ability of wildlife overpasses to provide connectivity and prevent genetic isolation. *Conservation Biology* 23: 548–556.

Cousse S, Janeau G (1992) Time budget and polyphasic activity in Wild boar (*Sus scrofa* L.). In: Spitz F, Janeau G, Gonzales G, Aulagnier S (eds) *Proceedings of the 'Ongulés/Ungulates 91' International Symposium*, 391–394. Société Francaise pour l'Etude et la Protection des Mammifères, Paris, and Institut de Recherche sur les Grands Mammifères, Toulouse, France.

Cousse S, Spitz F, Hewison M, Janeau G (1994) Use of space by juveniles in relation to their postnatal range, mother, and siblings: an example in the wild boar, *Sus scrofa* L. *Canadian Journal of Zoology* 72: 1691–1694.

Croney CC, Adams KM, Washington CG, Stricklin WR (2003) A note on visual, olfactory and spatial cue use in foraging behavior of pigs: indirectly assessing cognitive abilities. *Applied Animal Behaviour Science* 83: 303–308.

D'Andrea L, Durio P, Perrone A, Pirone S (1995) Preliminary data of the wild boar (*Sus scrofa*) space use in mountain environment. *Ibex Journal of Mountain Ecology* 3: 117–121.

Dardaillon M (1987) Seasonal feeding habits of the wild boar in a Mediterranean wetland, the Camargue (southern France). *Acta Theriologica* 32: 389–401.

Dardaillon M (1988) Wild boar social groupings and their seasonal changes in the Camargue, southern France. *Zeitschrift für Säugetierkunde* 53: 22–30.

Dardaillon M, Beugnon G (1987) The influence of some environmental characteristics on the movements of wild boar (*Sus scrofa*). *Biology of Behaviour* 12: 82–92.

D'Eath RB, Turner SP (2009) The natural behaviour of the pig. In: Marchant-Forde J (ed) *The Welfare of Pigs*, 13–45. Springer Science and Business Media, Dordrecht, Netherlands.

Dexter N (1998) The influence of pasture distribution and temperature on habitat selection by fetal pigs in a semi-arid environment. *Wildlife Research* 25: 547–559.

Dinter U (1991) *Das Raum-Zeitverhalten von Schwarzwild im Grunewald in den Sommermonaten Unter Besonderer Berücksichtigung Menschlicher Störungen*. Dissertation, Ludwig-Maximilian-Universität, Munich, Germany.

Erkinaro E, Heikura K, Lindgren E, Pulliainen E, Sulkava S (1982) Occurence and spread of the wild boar (*Sus scrofa*) in eastern Fennoscandia. *Memoranda Societatis pro Fauna et Flora Fennica* 58: 39–47.

Etienne AS, Maurer R, Seguinot V (1996) Path integration in mammals and its interaction with visual landmarks. *Journal of Experimental Biology* 199: 201–209.

Fagan WF, Lewis MA, Auger-Méthé M, Avgar T, Benhamou S, Breed G et al. (2013) Spatial memory and animal movement. *Ecology Letters* 16: 1316–1329.

Fernández-Llario P (2004) Environmental correlates of nest site selection by wild boar *Sus scrofa*. *Acta Theriologica* 49: 383–392.

Frantz AC, Bertouille S, Eloy MC, Licoppe A, Chaumont F, Flamand MC (2012) Comparative landscape genetic analyses show a Belgian motorway to be a gene flow barrier for red deer (*Cervus elaphus*), but not wild boars (*Sus scrofa*). *Molecular Ecology* 21: 3445–3457.

Gamelon M, Douhard M, Baubet E, Gimenez O, Brandt S, Gaillard J-M (2013) Fluctuating food resources influence developmental plasticity in wild boar. *Biology Letters* 9: 20130419. doi:10.1098/rsbl.2013.0419.

Garcia G, Vergara J, Lombardi R (2011) Genetic characterization and phylogeography of the wild boar *Sus scrofa* introduced into Uruguay. *Genetics and Molecular Biology* 34: 329–337.

Garland T (1983) The relation between maximal running speed and body mass in terrestrial mammals. *Journal of Zoology* 199: 157–170.

Gérard J-F, Cargnelutti B, Spitz F, Valet G, Sardin T (1991) Habitat use of wild boar in a French agroecosystem from late winter to early summer. *Acta Theriologica* 36: 119–129.

Gérard J-F, Cargnelutti B, Spitz F (1992) Relation entre anisotropie de l'occupation de l'espace et dispersion: un exemple chez le sanglier. *Mammalia* 56: 179–187.

Gethoffer F, Sodeikat G, Pohlmeyer K (2007) Reproductive parameters of wild boar (*Sus scrofa*) in three different parts of Germany. *European Journal of Wildlife Research* 53: 287–297.

Giraldeau L-A, Caraco T (2000) *Social Foraging Theory. Monographs in Behaviour and Ecology*. Princeton University Press, Princeton, New Jersey, USA.

Goulding MJ (2001) Possible genetic sources of free-living wild boar (*Sus scrofa*) in Southern England. *Mammal Review* 31: 245–248.

Graves HB (1984) Behavior and ecology of wild and feral swine (*Sus scrofa*). *Journal of Animal Science* 58: 482–492.

Gustafsson M, Jensen P, de Jonge F, Schurrman T (1999) Domestication effects on foraging strategies in pigs (*Sus scrofa*). *Applied Animal Behaviour Science* 62: 305–317.

Hammell DL, Kratzer DD, Bramble WJ (1975) Avoidance and maze learning in pigs. *Journal of Animal Science* 40: 573–579.

Harestad AS, Bunnell FL (1979) Home range and body weight – a re-evaluation. *Ecology* 60: 389–402.

Hebeisen C (2007) *Population Size, Density and Dynamics, and Social Organization of Wild Boar (*Sus scrofa*) in the Basin of Geneva*. PhD thesis, Université de Neuchâtel, Neuchâtel, Switzerland.

Held S, Baumgartner J, Kilbride A, Byrne RW, Mendl M (2005) Foraging behaviour in domestic pigs (*Sus scrofa*): remembering and prioritizing food sites of different value. *Animal Cognition* 8: 114–121.

Hessing MJC, Hagelsø AM, van Beek JAM, Wiepkema RP, Schouten WGP, Krukow R (1993) Individual behavioural characteristics in pigs. *Applied Animal Behaviour Science* 37: 285–295.

Hone J, Atkinson B (1983) Evaluation of fencing to control feral pig movement. *Australian Wildlife Research* 10: 499–505.

Howe TD, Singer FJ, Ackerman BB (1981) Forage relationships of European wild boar invading northern hardwood forest. *Journal of Wildlife Management* 3: 748–754.

Jachowski DS, Montgomery RA, Slotow R, Millspaugh JJ (2013) Unravelling complex associations between physiological state and movement of African elephants. *Functional Ecology* 27: 1166–1175.

Janeau G, Cousse S, Cargnelutti B, Spitz F (1995) Le rôle des déplacements journaliers dans l'organisation socio-spatiale des populations de sangliers (*Sus scrofa* L.). *Revue d'écologie* 50: 35–48.

Jankevicius ML, Widowski TM (2004) The effect of ACTH on pigs' attraction to salt or blood-flavored tail-models. *Applied Animal Behaviour Science* 87: 55–68.

Jansen J, Bolhuis JE, Schouten WP, Spruijt B, Wiegant V (2009) Spatial learning in pigs: effects of environmental enrichment and individual characteristics on behaviour and performance. *Animal Cognition* 12: 303–315.

Jędrzejewska B, Jędrzejewski W (1998) *Predation in Vertebrate Communities. The Białowieża Primeval Forest as a Case Study*. Springer-Verlag, Berlin, Germany.

Jędrzejewski W, Jędrzejewska B, Okarma H, Schmidt K, Zub K, Musiani M (2000) Prey selection and predation by wolves in Białowieża primeval forest, Poland. *Journal of Mammalogy* 81: 197–212.

Jerina K, Adamic M, Krze B (2005) Influences of topography and highway as migration barrier on dispersal patterns of wild boar (*Sus scrofa*) in Slovenia. In: Pohlmeyer KV (ed) *XXVIIth Congress of IUGB*, 133–135. Hannover, Germany.

Keuling O, Stier N, Roth M (2008a) Annual and seasonal space use of different age classes of female wild boar *Sus scrofa* L. *European Journal of Wildlife Research* 54: 403–412.

Keuling O, Stier N, Roth M (2008b) How does hunting influence activity and spatial usage in wild boar *Sus scrofa* L.? *European Journal of Wildlife Research* 54: 729–737.

Keuling O, Stier N, Roth M (2009) Commuting, shifting or remaining? Different spatial utilisation patterns of wild boar *Sus scrofa* L. in forest and field crops during summer. *Mammalian Biology – Zeitschrift für Säugetierkunde* 74: 145–152.

Keuling O, Baubet E, Duscher A, Ebert C, Fischer C, Monaco A et al. (2013) Mortality rates of wild boar *Sus scrofa* L. in central Europe. *European Journal of Wildlife Research* 59: 805–814.

Kittawornrat A, Zimmerman JJ (2011) Toward a better understanding of pig behavior and pig welfare. *Animal Health Research Reviews* 12: 25–32.

Krosniunas EH (1979) *Social Facilitation and Foraging Behavior of the Feral Pig,* Sus scrofa*, on Santa Cruz Island, California*. MSc thesis, University of California, Davis, California, USA.

Kuijper DPJ, Verwijmeren M, Churski M, Zbyryt A, Schmidt K, Jędrzejewska B, Smit C (2014) What cues do ungulates use to assess predation risk in dense temperate forests? *PLoS ONE* 9: e84607. doi:10.1371/journal.pone.0084607.

Kurz JC, Marchiton RL (1972) Radiotelemetry studies of feral hogs in South Carolina. *Journal of Wildlife Management* 36: 1240–1248.

Larson G, Dobney K, Albarella U, Fang MY, Matisoo-Smith E, Robins J et al. (2005) Worldwide phylogeography of wild boar reveals multiple centers of pig domestication. *Science* 307: 1618–1621.

Laughlin K, Mendl M (2000) Pigs shift too: foraging strategies and spatial memory in the domestic pig. *Animal Behaviour* 60: 403–410.

Leblond M, Dussault C, Ouellet J-P (2010) What drives fine-scale movements of large herbivores? A case study using moose. *Ecography* 33: 1102–1112.

Lemel J, Truve J, Soderberg B (2003) Variation in ranging and activity behaviour of European wild boar *Sus scrofa* in Sweden. *Wildlife Biology* 9: 29–36.

Lomas CA, Piggins D, Phillips CJC (1998) Visual awareness. *Applied Animal Behaviour Science* 57: 247–257.

Löttker P, Rummel A, Traube M, Stache A, Šustr P, Müller J, Heurich M (2009) New possibilities of observing animal behaviour from a distance using activity sensors in GPS-collars: an attempt to calibrate remotely collected activity data with direct behavioural observations in red deer *Cervus elaphus*. *Wildlife Biology* 15: 425–434.

Lozan A (1995) Study of the wild boar (*Sus scrofa* L.) memory in its orientative behaviour. *Ibex Journal of Mountain Ecology* 3: 130.

Maillard D, Fournier P (1995) Effects of shootings with hounds on home range size of wild boar (*Sus scrofa* L.) groups in Mediterranean habitat. *Ibex Journal of Mountain Ecology* 3: 102–107.

Mainland I, Schutkowski H, Thomson AF (2007) Macro-and micromorphological features of lifestyle differences in pigs and wild boar. *Anthropozoologica* 42: 89–106.

Massei G, Genov PV, Staines BW, Gorman ML (1997) Factors influencing home range and activity of wild boar (*Sus scrofa*) in a Mediterranean coastal area. *Journal of Zoology* 242: 411–423.

Mata C, Hervas I, Herranz J, Suarez F, Malo JE (2008) Are motorway wildlife passages worth building? Vertebrate use of road-crossing structures on a Spanish motorway. *Journal of Environmental Management* 88: 407–415.

Mauget R (1983) Home range use and its determining factors in the European wild boar (*Sus scrofa* L.). In: Anonymous (eds) *Proceedings of the XV Congreso Internacional Fauna Cinegética y Silvestre*, 315–329. Trujillo, Spain.

Mendl M, Laughlin K, Hitchcock D (1997) Pigs in space: spatial memory and its susceptibility to interference. *Animal Behaviour* 54: 1491–1508.

Mendl M, Held S, Byrne RW (2010) Pig cognition. *Current Biology* 20: R796–R798.

Morales JM, Moorcroft PR, Matthiopoulos J, Frair JL, Kie JG, Powell RA, Merrill EH, Haydon DT (2010) Building the bridge between animal movement and population dynamics. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365: 2289–2301.

Nathan R, Getz WM, Revilla E, Holyoak M, Kadmon R, Saltz D, Smouse PE (2008) A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences of the United States of America* 105: 19052–19059.

Nicol CJ, Pope SJ (1994) Social learning in sibling pigs. *Applied Animal Behaviour Science* 40: 31–43.

Nishii J (2006) An analytical estimation of the energy cost for legged locomotion. *Journal of Theoretical Biology* 238: 636–645.

Patterson TA, Thomas L, Wilcox C, Ovaskainen O, Matthiopoulos J (2008) State-space models of individual animal movement. *Trends in Ecology & Evolution* 23: 87–94.

Podgórski T, Baś G, Jędrzejewska B, Sönnichsen L, Śnieżko S, Jędrzejewski W, Okarma H (2013) Spatiotemporal behavioral plasticity of wild boar (*Sus scrofa*) under contrasting conditions of human pressure: primeval forest and metropolitan area. *Journal of Mammalogy* 94: 109–119.

Reidy MM, Campbell TA, Hewitt DG (2008) Evaluation of electric fencing to inhibit feral pig movements. *Journal of Wildlife Management* 72: 1012–1018.

Reilly SM, McElroy EJ, Biknevicius AR (2007) Posture, gait and the ecological relevance of locomotor costs and energy-saving mechanisms in tetrapods. *Zoology (Jena, Germany)* 110: 271–289.

Riotte-Lambert L, Benhamou S, Chamaillé-Jammes S (2013) Periodicity analysis of movement recursions. *Journal of Theoretical Biology* 317: 238–243.

Roshier DA, Doerr VA, Doerr ED (2008) Animal movement in dynamic landscapes: interaction between behavioural strategies and resource distributions. *Oecologia* 156: 465–477.

Rosvold J, Andersen R (2008) *Wild Boar in Norway – is Climate a Limiting Factor?* Norges Teknisk-naturvitenskapelige Universitet, Trondheim, Norway.

Russo L, Massei G, Genov PV (1997) Daily home range and activity of wild boar in a Mediterranean area free from hunting. *Ethology Ecology & Evolution* 9: 287–294.

Saïd S, Tolon V, Brandt S, Baubet E (2012) Sex effect on habitat selection in response to hunting disturbance: the study of wild boar. *European Journal of Wildlife Research* 58: 107–115.

Saunders G, McLeod S (1999) Predicting home range size from the body mass or population densities of feral pigs, *Sus scrofa* (Artiodactyla: Suidae). *Australian Journal of Ecology* 24: 538–543.

Scandura M, Iacolina L, Crestanello B, Pecchioli E, Di Benedetto MF, Russo V, Davoli R, Apollonio M, Bertorelle G (2008) Ancient vs. recent processes as factors shaping the genetic variation of the European wild boar: are the effects of the last glaciation still detectable? *Molecular Ecology* 17: 1745–1762.

Scillitani L, Monaco A, Toso S (2010) Do intensive drive hunts affect wild boar (*Sus scrofa*) spatial behaviour in Italy? Some evidences and management implications. *European Journal of Wildlife Research* 56: 307–318.

Singer FJ, Otto DK, Tipton AR, Hable CP (1981) Home ranges, movements, and habitat use of European wild boar in Tennessee. *Journal of Wildlife Management* 45: 343–353.

Singh NJ, Börger L, Dettki H, Bunnefeld N, Ericsson G (2012) From migration to nomadism: movement variability in a northern ungulate across its latitudinal range. *Ecological Applications* 22: 2007–2020.

Sodeikat G, Pohlmeyer K (2003) Escape movements of family groups of wild boar *Sus scrofa* influenced by drive hunts in Lower Saxony, Germany. *Wildlife Biology* 9: 43–49.

Sodeikat G, Pohlmeyer K (2007) Impact of drive hunts on daytime resting site areas of wild boar family groups (*Sus scrofa* L.). *Wildlife Biology in Practice* 3: 28–38.

Spencer PBS, Hampton JO (2005) Illegal translocation and genetic structure of feral pigs in Western Australia. *Journal of Wildlife Management* 69: 377–384.

Spitz F (1992) General model of spatial and social organization of the wild boar (*Sus scrofa*). In: Spitz F, Janeau G, Gonzalez G, Aulagnier S (eds) *Proceedings of the 'Ongulés/Ungulates 91' International Symposium*, 385–389. Société Francaise pour l'Etude et la Protection des Mammifères, Paris, and Institut de Recherche sur les Grands Mammifères, Toulouse, France.

Spitz F, Janeau G (1990) Spatial strategies: an attempt to classify daily movements of wild boar. *Acta Theriologica* 35: 129–149.

Spitz F, Janeau G (1995) Daily selection of habitat in wild boar (*Sus scrofa*). *Journal of Zoology* 237: 423–434.

Studnitz M, Jensen MB, Pedersen LJ (2007) Why do pigs root and in what will they root? A review on the exploratory behaviour of pigs in relation to environmental enrichment. *Applied Animal Behaviour Science* 107: 183–197.

Suselbeek L, van Wieren SE, Jansen PA, Bongers FJJM, Prins HHT (2012) Is oak regeneration doomed after wild boar populations boomed? In: Keuling O (ed) *Proceedings of the 9th International Symposium on Wild Boar and other Suids*, 3. Institute for Terrestrial and Aquatic Wildlife Research, University of Veterinary Medicine, Hannover, Germany.

Thurfjell H, Ball JP, Åhlén PA, Kornacher P, Dettki H, Sjöberg K (2009) Habitat use and spatial patterns of wild boar *Sus scrofa* (L.): agricultural fields and edges. *European Journal of Wildlife Research* 55: 517–523.

Thurfjell H, Spong G, Ericsson G (2013) Effects of hunting on wild boar *Sus scrofa* behaviour. *Wildlife Biology* 19: 87–93.

Thurfjell H, Spong G, Ericsson G (2014) Effects of weather, season, and daylight on female wild boar movement. *Acta Theriologica* 59: 467–472.

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

Tolon V, Dray S, Loison A, Zeileis A, Fischer C, Baubet E (2009) Responding to spatial and temporal variations in predation risk: space use of a game species in a changing landscape of fear. *Canadian Journal of Zoology* 87: 1129–1137.

Truve J (2004) *Pigs in Space: Movement, Dispersal and Geographic Expansion of the Wild Boar (*Sus scrofa*) in Sweden*. PhD thesis, Göteborgs Universitet, Göteborg, Sweden.

Truve J, Lemel J (2003) Timing and distance of natal dispersal for wild boar *Sus scrofa* in Sweden. *Wildlife Biology* 9: 51–57.

Truvé J, Lemel J, Söderberg B (2004) Dispersal in relation to population density in wild boar (*Sus scrofa*). *Galemys* 16: 75–82.

Újváry D, Horváth Z, Szemethy L (2012) Effect of area decrease in a food competition situation in captive wild boars (*Sus scrofa*). *Journal of Veterinary Behavior: Clinical Applications and Research* 7: 238–244.

Urbano F, Cagnacci F, Calenge C, Dettki H, Cameron A, Neteler M (2010) Wildlife tracking data management: a new vision. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 365: 2177–2185.

Wagner C, Holzapfel M, Kluth G, Reinhardt I, Ansorge H (2012) Wolf (*Canis lupus*) feeding habits during the first eight years of its occurrence in Germany. *Mammalian Biology – Zeitschrift für Säugetierkunde* 77: 196–203.

Wevers J-P, Scherer P-C, Berger A, Blaum N, Fischer C, Jeltsch F, Schröder B (2011) Identifying movement behaviour from 3-dimensional acceleration data for European brown hares

(*Lepus europaeus*) and wild boars (*Sus scrofa*). *8th International Conference on Behaviour, Physiology and Genetics of Wildlife*, Berlin, Germany.

Whishaw IQ, Hines DJ, Wallace DG (2001) Dead reckoning (path integration) requires the hippocampal formation: evidence from spontaneous exploration and spatial learning tasks in light (allothetic) and dark (idiothetic) tests. *Behavioural Brain Research* 127: 49–69.

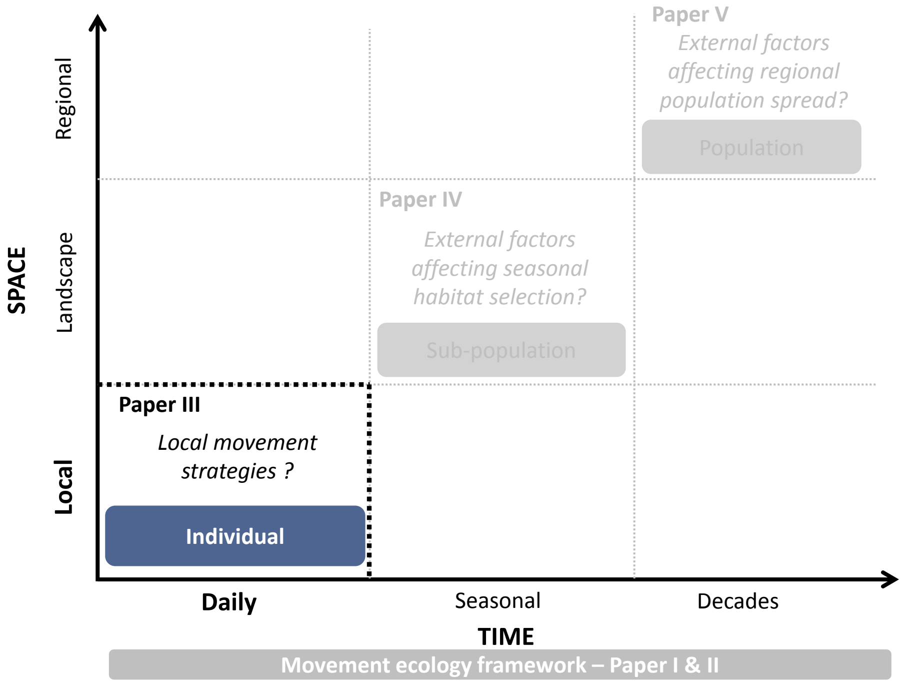
Wilson RP, Quintana F, Hobson VJ (2012) Construction of energy landscapes can clarify the movement and distribution of foraging animals. *Philosophical Transactions of the Royal Society of London B Biological Sciences* 279: 975–980.

With K (1994) Using fractal analysis to assess how species perceive landscape structure. *Landscape Ecology* 9: 25–36.

Zaĭtsev VA (1996) The synchronization of behavior and individual distances in groups of wild boars (*Sus scrofa* L.). *Zhurnal Obshchei Biologii* 53: 243–257.

Zonderland JJ, Cornelissen L, Wolthuis-Fillerup M, Spoolder HAM (2008) Visual acuity of pigs at different light intensities. *Applied Animal Behaviour Science* 111: 28–37.

A.3 PAPER III



Morelle K, Bunnefeld N, Oswald SA, Lejeune P From GPS tracks to fine-scale, behavioural movement strategies: a straightforward approach for identifying multiple spatial behaviours. *Manuscript*

From GPS tracks to fine-scale, behavioural movement strategies: a straightforward approach for identifying multiple spatial behaviours

Kevin Morelle, Gembloux Agro-Bio Tech, University of Liège, passage des déportés 2, 5030 Gembloux, Belgium, morelle.k@gmail.com

Nils Bunnefeld, Biological and Environmental Sciences, School of Natural Sciences, University of Stirling, Stirling, FK9 4LA, UK

Stephen Oswald, Division of Science, Penn State University, Berks Campus, Reading, PA 19610, USA.

corresponding author: Kevin Morelle

Abstract

Thanks to the continuing development of animal tracking tools, such as GPS devices, detailed data on the movement tracks of individual animals are now attainable for many species. However, straightforward methods to decompose GPS tracks into meaningful spatial behaviours occurring at small scalesare currently lacking. We develop an analytical approach that combines separately-validated methods into a powerful tool for decomposing animal GPS tracks and classifying short-range movements. Decomposition of tracks is achieved through detection of structural changes in movement behavior using behavioural change point analysis. The net squared displacement of subsequent segments is then classified into movement strategies based on the fit of competing linear and nonlinear least squares regression models.
We illustrate our approach for movement of three wild boar *Sus scrofa* tracked using GPS collars that reported fixes at 15 min intervals. Our approach successfully classified 81% of the tracks into meaningful behavioral states that persisted for between 1.2 and 31.2 hours. We detected four main spatial behaviours (area restricted search, central place foraging, nomadism and dispersing) which corresponded well with previous reports of the movement ecology of boar in our study area and demonstrate a high diversity in spatial strategies for this species. Our results validate this approach for classifying tracking data into high-resolution movements over short temporal scales.

Keywords: behavioral change point analysis, fine scale movement, net squared displacement, FlexParamCurve, , wild boar

Introduction

The development and use of tracking technology for a multitude of species worldwide has resulted in high resolution movement data which has greatly improved our understanding of animal spatial ecology [1]. This, in turn, has facilitated more effective conservation efforts and management strategies for endangered [2] or pest species [3]. Many animals are almost continuously on the move for different purposes, e.g. feeding, avoiding predators, following conspecifics, or dispersing. Recent research has resulted in the emergence of the movement ecology paradigm [4]: an integrated approach to understand animal movement based on interactions among its internal state, motion capacity, navigation capacity and the environment. This provides a useful predictive framework to investigate numerous questions related to these different components of animals' lives. Our understanding of animal movement is, however, highly dependent on methods for comprehensive analysis of extensive, high resolution, time series data.

Detailed understanding of long-term tracks, i.e. knowing what precisely what animal are doing over short spatial and temporal scale, is required since these short range processes (e.g. feeding, dispersing, exploring, mating or escaping [5, 6]) actually drive the fitness of individuals and influence population distribution [7, 8]. Integrated analysis of an animal movement path is a two steps process involving firstly track segmentation and secondly segment classification. Diverse methods exist to segment (record a high likelihood that an animal has changed behavior) animal tracks into shorter spatial and temporal behavioral states: for example clustering or filtering techniques [9-11] and statistical description of movement parameters (e.g. behavioural change point analysis [12]). These methods essentially group segments of the data representing similar movement patterns by matching their expected structure against a time series' of various parameters, e.g. step length (distance between successive GPS points) and turning angle (direction change between two successive steps), derived from animal relocations. Most commonly, segmentation methods try to remove one dimension of analysis (usually a spatial dimension) to facilitate one-dimensional time-series analysis. To do so, they convert consecutive animal relocation (x_t, y_t) into movement parameters, e.g. speed, azimuth, turning angle, and plot it in the shape of time series with the aim of detecting natural breakpoint assumed to represent behavioral change of the individual. Though this approach has been successful in segmenting animal tracks it often misses a clear classification of the movement strategy performed by the animal. Most of these methods are not able to suggest underlying behavioral patterns (i.e. what the animal is doing and what kind of behavior is involved). Commonly, segmentation methods simply describe the segment based on the movement parameters the segmentation was built up, e.g. fast/slow and straight/sinuous segment when based on speed and turning angle [13], or adopt a simplistic binary view of animal spatial abilities, e.g. foraging/travelling, foraging /resting [14] or intensive/extensive search [15] or over small scale (foraging vs. non foraging movement) and large scale (migratory vs. non-migratory). Moreover, existing methods are often based on complex statistics, require extensive computer processing [16] or are based on highly recursive point sampling not always available when tracking large mammals over long time scale.

Once an animal track has been segmented, the next step involves identifying the relative behavioral states to which the segment corresponds. Going further than simple composite classification as exemplified above is a difficult task because states i) are dependent on a large number of internal, i.e. motivation, navigation and motion capacity, and external factors [4], ii) vary according to spatial and temporal scales considered [17]. Conversion of animal tracks into meaningful movement strategies has been achieved through use of mixed movement models [18], state-space models [19] behavioral movement segmentation [16] and behavioral state augmentation [20]. However, all these methods are based on complex statistical models, often not easily accessible to biologists, and have restrictive assumptions that make them unsuitable for most datasets (Table 1). + or require simplification algorithm and high sampling rate [13] not always available when tracking large mammals, while some other doesn't take autocorrelation into account though successive animal relocation are per definition autocorrelated. +applied to detect movement over broad scale, e.g. migration but not fine scale changes [21]. Though these methods considerably improve our understanding of animal interaction with their environment, none really offers an integrated approach that take into account the wide range of movement strategies an animal is able to perform.

Here, we use a user-friendly analytical approach combining separately-validated methods to develop a powerful tool for segmenting and classifying animal GPS tracks into short-range movement strategies. We first segment the data using behavioral change point analysis [12] and then classify behavior by fitting competing linear and non-linear curves [22, 23] to the net squared displacement in each segment. This is easily executed in currently available software, has less restrictive assumptions than existing methods, and is combines already-validated approaches for analyzing movement data. We illustrate the strength of this approach for movement track data from wild boar *Sus scrofa* tracked by GPS through agro-forest landscapes.

Materials and Methods

Our new analytical approach uses a straight-forward, two-step process to decompose the GPS track: i) the entire animal track is split into segments using behavioral change point analysis [12], ii) net squared displacement is calculated and classified by linear and non-linear least squares (nls) curve-fitting [22-24].

Step 1: Segmenting GPS track into short trips

We applied behavioral change point analysis (BCPA) to automatically segment the complete GPS tracks [12]. This method converts raw GPS data (sequential, temporal latitude and longitudinal positional fixes) into a time-series' of step length and turning angle and then further transforms these into orthogonal persistence velocity (the magnitude of movement) and turning velocity (tendency toward a particular direction) [12]. As well as providing meaningful movement parameters, this new time-series can be modeled as a stationary, Gaussian, autoregressive process [12]. BCPA assumes that any significant change in parameters (either mean, variance or continuous autocorrelation) of the time-series represents a change in the animal state. Such changes are assessed via a user-defined, moving window passed in which significant structural shifts between homogenous patterns are assessed [12]. Identification of change points is based on the weight of statistical evidence for a change in the mean, variance and continuous autocorrelation using Bayesian Information Criterion (BIC). If a change point is identified, its location is recorded. The window is then shifted forward by one data point and the operation is repeated. Once the entire track has been analyzed, the parameters on either side of change point locations are averaged across all moving windows to maximize change point detection [12].

Detection of changing point is sensible to the temporal range over which changing points are observed. This range is measured by the clusterwidth parameter, corresponding to the bandwidth of the density of the break distribution [25]. Since we had no prior information on the outcome of the BCPA we tested various values of clusterwidth to observe what temporal scale of movement is detected. We used detected change points to segment GPS tracks (the original raw data) into multiple, shorter segments associated with potentially different behaviors. We tested values ranging from 1 to 5 which gave a range of segment lengths from 4.3±2.2 hours to 42.0±22.1 hours (Table 1).

Table 1. Effect of clusterwidth parameters on the temporal resolution and size (number of fixes) of detected segments. Values are means across all three tracked individuals.

Clusterwidth	Length of identified segment (hours)		Number of positional fixes	
	mean	sd	mean	sd
1	4.3	2.2	17	8
2	6.5	2.6	26	10
3	10.6	5.0	40	18
4	19.4	9.8	74	37
5	42.0	22.1	156	85

We opted for a clusterwidth of 3 to permit analysis of movement at the half-day scale (Fig. 2), also ensuring a sufficient number of relocations per segment [14].

Step 2: Movement modelling

We then calculated net squared displacement (NSD) separately for each segment [27]. NSD, which is the Euclidian squared distance between the first location of a segment and any consecutive relocations [26], is an effective method to characterize GPS data because it transforms movement data from 3D (x, y, t) to 2D (x from origin, t) permitting the application of simpler statistical models [24]. Recently, modelling net squared displacement of animal over time has been used successfully to characterize patterns of movement of migratory animals over large distances [6, 22, 27] [24]. Despite its success at modelling movement of animals at very large scales, this approach has rarely been applied at smaller spatio-temporal scales [14] and is still dependent on visual analysis (see [28, 29]) for classification.

To classify segments into behavioural movements, we modified the model-driven approach of Bunnefeld *et al.* [22] to permit analysis of movements performed at finer scale. To model NSD over short temporal scales, we assumed that behavior observed at large scales (i.e. residency, migrating, nomadism, dispersing [22]) also occur at daily scales within an animal's home range. To classify segments correctly, the user must first decide on a candidate set of ecologically-appropriate movement strategies to select between. As in information theoretic model selection approaches (Burnham and Anderson 2002), correct and comprehensive selection of candidate models is vital to ensure that segments are correctly categorized. If a strategy is omitted from the candidate set it cannot be identified by subsequent model selection and thus will prevent complete classification of behavioural strategies. For wild boar we identify four broad movement strategies (circular, dispersal, nomadic and residency Fig 1). While resident behaviour over large scale describes non migrating animal, over short scale, we define **residency** as movement performed in the vicinity of the starting point, and that can be assimilated as area restricted search behaviour [30] (Fig.1). **Circular** or partially circular movement are short-range migratory behaviour related to central place foraging and consists of longer movements away from the bedding site followed by a return to this starting location [31] (Fig.1). **Nomadism** and **dispersing** are both behaviors leading animals away from an initial starting point with no return (Fig.1). They differ in the initiation of the movement process, being a gradual linear increase in the distance to the starting point for nomadism and a fast and directed movement followed or preceded by slow movements for dispersing [32] (Fig 1).

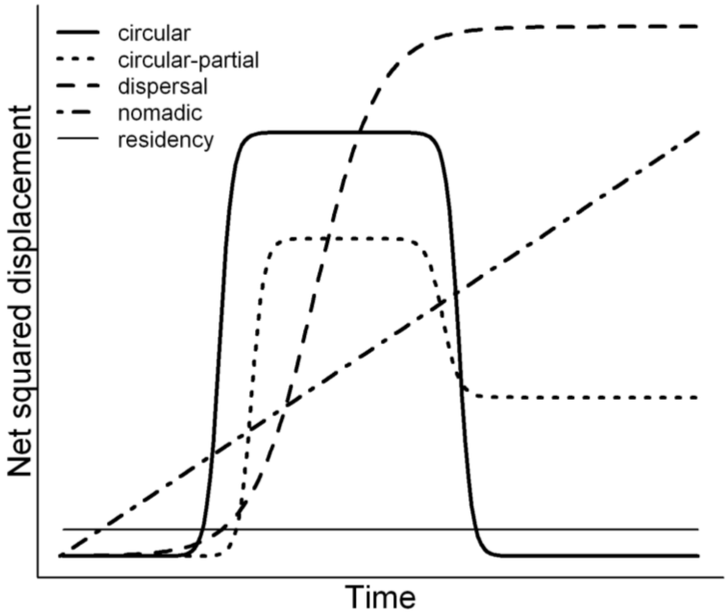


Figure 1. Expected movement strategies chosen to illustrate analytical method using wild boar movement data (adapted from Bunnefeld *et al.* [22] to be appropriate for small scale movements. For description of the different movement strategies see text).

Before classifying segments into behavioral movement strategies, we excluded stationary segments (those representing the residency behavior), those with a maximum NSD < mean location error, estimated from the literature at a value of 20 m [33, 34]. In total across the three observed individuals, we excluded 13.6% of stationary segments. For the remaining segments, we statistically classified movement strategy for each behavioral segment by fitting three candidate models (one nonlinear and two linear models) to predict NSD as a function of time. To model complex movement strategies (circular and dispersing behavior), we used reductions from an 8-parameter nonlinear equation (double Richards curve) :

$$NSD = \frac{A}{1 + m \cdot \exp(-k(t-i))^{1/m}} + \frac{A'}{1 + m' \cdot \exp(-k'(t-i'))} \qquad \text{(Eqn. 1)}$$

where A is the asymptote, t the time since start of the trip, k the rate parameter, i is the inflection point, m the shape parameter for the increasing portion of the curve and A', k' and i' are their equivalent parameters for the subsequent decreasing portion of the curve [23]. By fixing redundant parameters as constants, we developed the most appropriate reduced curve equation [23] to model a variety of behaviors. Since we could predict the shape of expected behaviors *a priori* (Fig 1) we chose the following models available in the *FlexParamCurve* package of R: #32 [3-parameter logistic] (for dispersal behavior) and #2 [7-parameter Richards] [23] (for circular behavior). These selected curves were then initially parameterized using the *modpar()* function *FlexParamCurve* package [23] in R to optimize model convergence.

The linear equations took two forms. First:

$$NSD = at \qquad \text{(Eqn. 2)}$$

with t corresponding to the time since departure and a to the slope parameter. This equation represented the nomadic movement strategy (a gradual increase in NSD). The second linear equation was an intercept-only model:

$$NSD = c \qquad \text{(Eqn. 3)}$$

where c is a constant and the relation is expected to represent residency movement.
The linear equations were fitted by least squares regression in R [35].

Goodness of fit for each of the three candidate models was assessed for each segment using the Akaike Information Criterion (AIC) and Concordance Criterion (CC) [6, 36], which outperforms traditional goodness of fit measures in the case of non-linear models [36]. CC values fall between -1 (perfect negative fit) and 1 (perfect positive fit) for the concordance between observed and predicted values. If convergence failed for any non-linear model it was assigned a CC value of 0.

Since intercept model (linear Eqn 3) give CC value of zero, we firstly discriminated residency behavior based on the combined AIC (lowest from the four models) and CC value (equal to zero). For the remaining segments, the model with the highest CC value was accepted as most appropriate but models with CC values > -0.7 or < 0.7 were determined to be failed classification cases. Then if linear Eqn 2 gave the best fit it was classified as nomadic behavior. If the non-linear model provided the best fit, to further distinguish between dispersal and circular movement strategies, we extracted three parameters from the fitted curve: distance from origin at the end of the trip (distEnd), the peak distance (largest distance from origin in the behavioral segment: peakD) and the ratio distend/peakD. If distEnd ≥ peakD, we classified movement as dispersal behavior. Because dispersing events can occur at various spatial scales, we further classified these into short-, medium-, or long-dispersal movements by calculating the minimum total within-cluster variance (using Ward's minimum variance hierarchical clustering [37] implemented in *hclust()* in R [35]) based on the error sum of squares. If distEnd < peakD, we classified the segment as a circular movement behavior and further categorized it as either a complete loop (distEnd/ peakD < 0.2) or incomplete loop (distEnd/ peakD > 0.2).

Testing the method: A case study on wild boar movements

We illustrate our approach using movement data from wild boar, a species known to exhibit many, complex movements and a high spatial plasticity [38, 39]. In our agricultural study area (Wallonia, Belgium [50°25'N, 4°53'E]; an agricultural area with small-to-moderate sized forest stands [1-20 ha]), boar can adapt to the seasonal dynamics of resources provided alternatively by crops and forests by appropriate movement strategies [40] which has large economic significance in terms of consequent crop damage.

We use GPS data collected from three subadult males. The animals were caught in Autumn 2011 and tagged with GPS/GSM Plus 3D collar (Vectronics Aerospace GmbH). To avoid effect of hunting disturbances [41, 42], we only used tracking data collected between 1st of January and 31st of April 2012. During this period, a total of 8265, 7968 and 8491 positional fixes for each tracked individual were recorded, each fix separated by 15 min intervals.

Raw GPS data were "cleaned" by removal of locations presenting error estimated. Specifically, we used a method based on unlikely distances moved within the sampling interval (15 min in our case) and erroneous spike, described as unlikely back and forth movement of the animal (determined by certain speed and turning angle) [43]. We specified these parameters as followed: maximum moved distance to 2 km, speed to 1.5 m/s and angle spike to 180º, and consecutively removed 1.5% of the total number of locations.

We followed the method described above to segment and classify the tracks into spatial movement strategies. Subsequently, we analyzed the scale at which they occurred, i.e. within or outside the home range boundaries. To do this we calculated, for every individual, the distance of every location from the barycenter (mean x, mean y) and took as home range limit the 95% quantile of theses distances [44].

Results

BCPA spell out

The BCPA highlighted 202, 197 and 210 break points, respectively, for each of the individuals (#1, #2, #3). These break points were used to split the whole track into shorter behavioral segments (Fig 3).

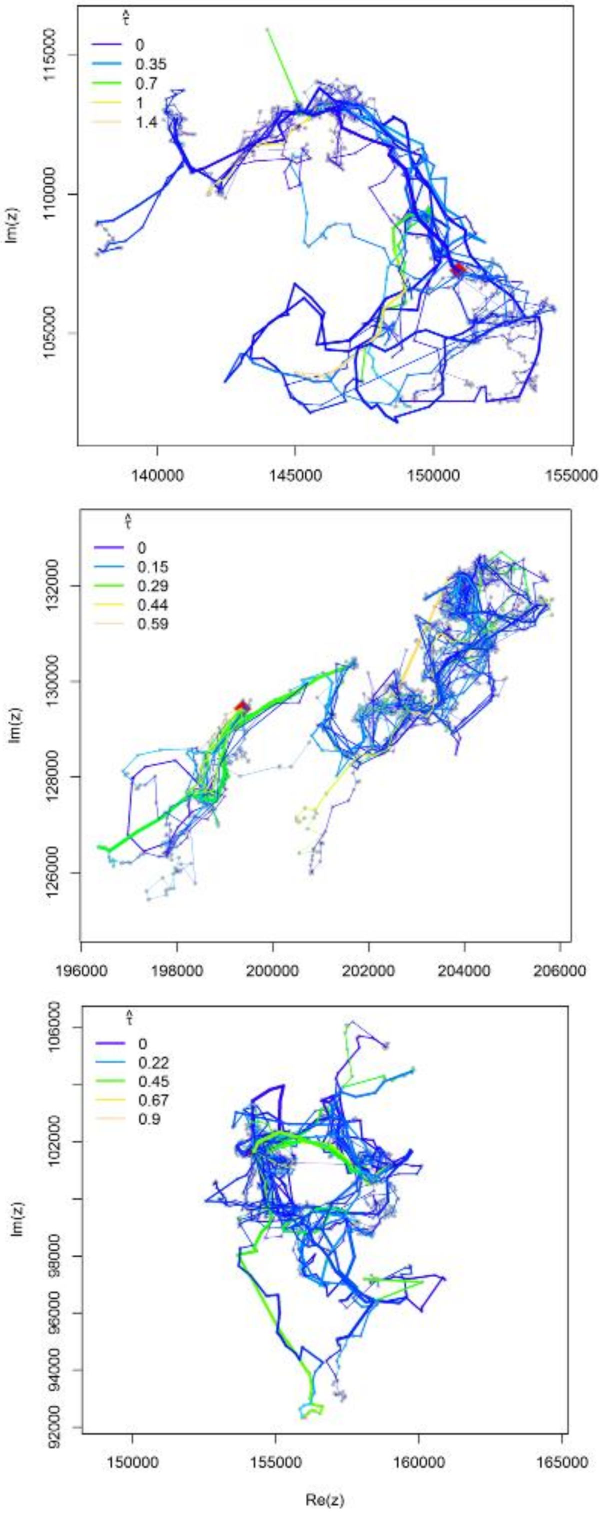


Figure 2. Smoothed (averaged over all estimated parameters [45]) trajectory of the whole track of three wild boar (#1, #2, #3) recorded between January and April 2012. Each categorized segment has a different value of Tau (color-coded) indicating the timescale/auto-correlation from BCPA. Segment width is proportional to the estimated mean persistence velocity.

Movement strategies

Comparing the two nonlinear models used, the 3-parameter logistic (Equation XX) gave higher fitting success than the XX (Eqn XX) (Fig.4).

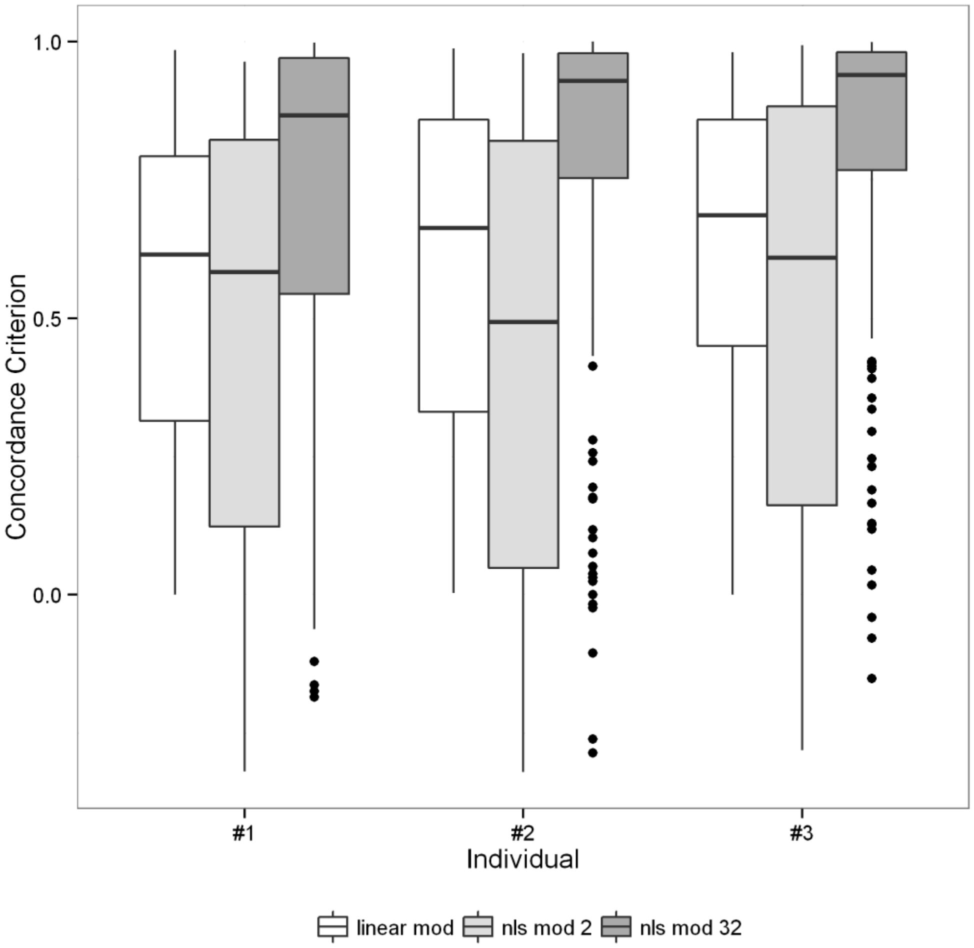


Figure 3. Comparison of the concordance criterion (CC) between the tested models: the linear nomadic model (linear mod) and the non linear #32 [3-parameter logistic] and #2 [4-parameter Richards] models [23]. Note that the intercept model (residency behavior) is not shown since this model could only be assessed by means of Akaike Information Criterion.

In total, 81% of segments were adequately classified into meaningful movement behaviors (Fig 6) (absolute CC value > 0.7). This represents 422 of the 521 segments (not including stationary behaviour) over the three individuals. Of those adequately classified, for wild boar #1, 15% were classified as residency behavior, 8% were nomadic movement behavior (Eqn 4, Fig 1), 38% were dispersal behavior (nonlinear equation, distEnd ≥ peakD, Fig 1) and 39% were either circular or partially-circular movement behaviors (nonlinear equation, distEnd < peakD, Fig 1). For the wild boar #2 we observed the following sequence: 5% residency, 8% nomadic, 64% dispersal, 23% circular/partially circular. For wild boar #3: 8% residency, 8% nomadic, 46% dispersal, 38 circular/partially circular Behavioral segments durations ranged between 3.5-26.7 hours for wild boar #1, 1.2-31.2 hours for wild boar #2 and 1.5-27.2 hours for wild boar #3.

We further distinguished among dispersal strategies based on the scale at which movement occurred. Dispersal events ranged between 0.2 and 9.9 km with 43% were classified as short dispersal, 6% as medium dispersal and 1% as long-distance dispersal (Table 1, supporting information S1). Residency, circular full and short dispersal occurred within the home range boundaries while, depending on the individual, the other strategies could lead the animal outside of this limit (Fig.4).

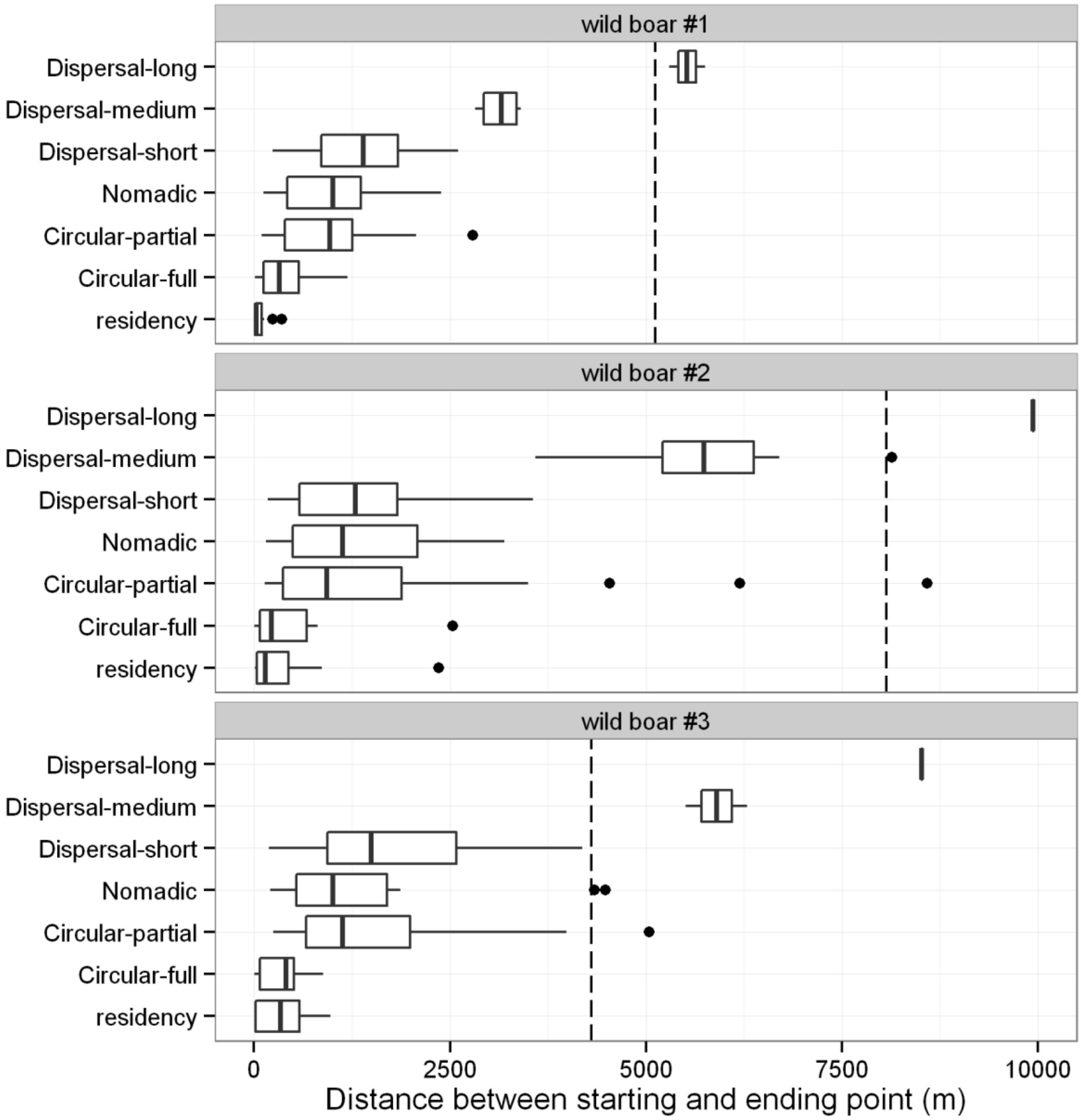


Figure 4. Comparison of the different movement strategies according to distance between the starting and the ending point. The dashed (---) vertical line indicates for each individual, the limit of the home range scale (see Method section).

The total distance travelled and speed reached their minimum and maximum in respectively the residency (1.2-3.8 km and 0.04-0.08 m/s) and the long dispersal behaviour mode (8.9-21.9 km and 0.32-0.76 m/s) (Table 1, supporting information S1). Though segment classified occur over a wide temporal range (1.2-31.2 hours), the average observed range was of 10.4±4.7

hours, roughly the half-daily scale. Among the spatial strategies delineated, we observed important variation between the three tracked wild boar, potentially suggesting the importance of individual variability (Fig.5).

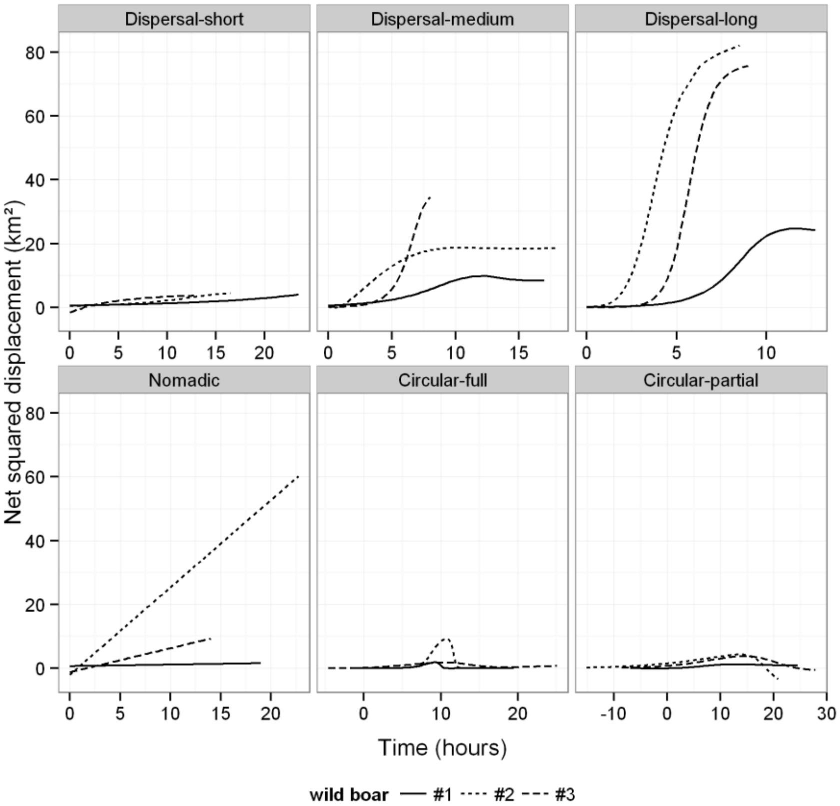


Figure 5. Fitted curves of Net Squared Displacement over time for the different identified behavioral segments.

Discussion

In this study we provide a straightforward analytical framework, using existing and validated techniques, to facilitate segmentation and classification of animal GPS track into high resolution (short temporal and spatial scale) behavioral states. In 81% of the cases, the segments extracted from GPS fixes of free-ranging wild boar could be successfully classified into 7 different movement strategies in four general movement types. Though the used sample is relatively small, we found consistency in frequency and patterns among the spatial strategies used by the different individuals. These strategies or states occur at various spatial, within and outside the home range, and temporal scale (hourly to daily). Specifically these states related to common spatial behavior observed in animal, such as dispersal, residency (i.e. area restricted search), nomadic and central place behaviors [32, 46]. If we consider stationary behavior, our approach successfully disentangles GPS tracks of animal into 8 states. Currently (see Table 1) most analytical method to segment and/or classify are restricted to 2-4 behavioral patterns (see table 1).

Until recently, analysis of animal space use was restricted to home range analyses or analyzing paths (straight lines between a starting and ending point). Improvements in tracking technology have extended this view of animal space use by allowing collection of fine scale movement data. Over the last fifteen years, numerous methods have been developed to improve our understanding of animal movement. However, the classification of such tracking data into meaningful, short-scale movement behaviors has been only achieved using complex and restrictive analytical techniques. In other studies, the segment length, duration and the success rate of classification is often missing. Moreover our approach is based on relatively few assumptions and Compared to other methods we did not fixed arbitrary an initial and ending point for the segment [14].

Our approach only requires assumption of the behavioral change point analysis, as to know the variable used (here the persistence velocity) follows a stationary continuous-time Gaussian process [45]. Though this assumption is not inherent to all movement data, a diagnostic of the BCPA model residuals can easily be implemented to check whether a normality assumption is satisfied. The main advantages of the BCPA method are that it considers correlation in the movement data over a certain temporal range and does not require a priori assumptions on behavioral categories. However, BCPA still requires parameters tuning, it is dependent of the temporal scale, resolution and the error linked to the movement data set used [45]. We showed in the present study, how the clusterwidth parameter affected temporal resolution of the BCPA output.

By means of linear and nonlinear regression of the net squared displacement we could classify segments extracted from the BCPA analysis into movement strategies. Nonlinear regression has successfully been used in other studies to model long distance movement of animal at the yearly scale [6, 22]. However, the method was primarily based on visualization to disentangle among animal spatial strategies. While differentiating among migratory or non-migratory animal based on NSD is relatively easy, applying the method over short scale where more spatial patterns requires a more automatic procedure. We showed with this study that the method could be effectively applied to lower scale movement processes without using eye-vizualization.

Our method could be extended to any other potential relation between NSD-time since regression method to model complex relation is now available [23]. Depending on potential existing behavior one could imagine extend the model to other varieties of NSD-time relation since the relative flexibility of nonlinear regression made it possible. The results of the nls analysis suggested that a minimum number of six relocations could already be used to model animal movement. Low sample rate (4-6/day) as often perform in terrestrial mammal tracking as to get year-round information of animal space use could already be modelled by mean of our approach.

We found result consistent with current knowledge of wild boar spatial ecology. Indeed, the large temporal range observed (1-30 hours) corresponds to what has been previously observed in free-ranging wild boar, with important variability in the duration of active bouts [47]. The number of states observed and the differences among the three individuals boars tracked confirm the high important behavioral heterogeneity of the species. The results of these study confirm and extend previous findings on the spatial strategies performed by wild boar at the daily scale [31]. The advantage of our approach is based on a automatic, assumption-free and repeatable method. We classified between 2-4 times more partial than complete circular movement. This result is in agreement with the known behavior of wild boar that use multiple resting sites within their home range [48, 49], rather than being central place foragers that return to their initial starting position.

In the case of wild boar, the option to limit the classification process to segments for which a mean net displacement higher than 20m of distance, estimated as or mean location error, considering this segment as part of a ‘stationary state’. Under this threshold scale, wild boar if not stationary can perform foraging search, an experimental study has shown that at low scale the search strategy of wild boar was mostly driven by random processes [50]. Moreover, in the specific case of wild boar, estimation of population level movement patterns can help managers to develop efficient strategies to control the population in sensible agro-forested landscapes. Our approach if combined with results of studies on the effect of hunting on wild boar movement [42, 44] could significantly improve our ability to …

In the field of movement ecology, it would be interesting to combine the outcome of our study with explanatory analysis of the external, i.e. the direct environment, and internal (e.g. energetic or stress constrains, if sensor are available on the tag) factors influencing the observed movement behaviors. What promote a strategy over the other? Individual variability, landscape context, local disturbances? include seasonal changes, comparison between different context [18], different species. Using our approach also allow to directly take into account individual variability, and possibly could highlight the role of temperament in the observed behavior, a factor shown to be important in the movement pattern of animal at large and small scales [22, 51]. In which habitat are a particular strategy used? At which time of the day? Are movements out of the home range related to natal dispersal? Now understanding why and under which circumstances a strategy is chosen over another is the next exciting challenge. Our result prove that combined used of a robust segmentation method such as bcpa, able to detect complex behavioural patterns, combined to the ability of net squared displacement to provide good description of animal movement [24] offers a unique opportunity to increase our understanding of animal movement over short scale.

References

1. Cagnacci F, Boitani L, Powell RA, Boyce MS: **Animal ecology meets GPS-based radiotelemetry: a perfect storm of opportunities and challenges.** *Philosophical Transactions of the Royal Society B: Biological Sciences* 2010, **365:**2157-2162.

2. Cooke SJ: **Biotelemetry and biologging in endangered species research and animal conservation: relevance to regional, national, and IUCN Red List threat assessments.** *Endangered Species Research* 2008, **4:**165-185.

3. Adams AL, Recio MR, Robertson BC, Dickinson KJM, van Heezik Y: **Understanding home range behaviour and resource selection of invasive common brushtail possums (Trichosurus vulpecula) in urban environments.** *Biol Invasions* 2014, **16:**1791-1804.

4. Nathan R, Getz WM, Revilla E, Holyoak M, Kadmon R, Saltz D, Smouse PE: **A movement ecology paradigm for unifying organismal movement research.** *Proceedings of the National Academy of Sciences of the United States of America* 2008, **105:**19052-19059.

5. Fryxell JM, Hazell M, Börger L, Dalziel BD, Haydon DT, Morales JM, McIntosh T, Rosatte RC: **Multiple movement modes by large herbivores at multiple spatiotemporal scales.** *Proceedings of the National Academy of Sciences* 2008.

6. Singh NJ, Börger L, Dettki H, Bunnefeld N, Ericsson G: **From migration to nomadism: movement variability in a northern ungulate across its latitudinal range.** *Ecol Appl* 2012, **22:**2007-2020.

7. Hawkes C: **Linking movement behaviour, dispersal and population processes: is individual variation a key?** *J Anim Ecol* 2009, **78:**894-906.

8. Getz WM, Saltz D: **A framework for generating and analyzing movement paths on ecological landscapes.** *Proceedings of the National Academy of Sciences* 2008, **105:**19066-19071.

9. Dodge S, Weibel R, Lautenschütz A-K: **Towards a Taxonomy of Movement Patterns.** *Information Visualization* 2008, **7:**240-252.

10. Enguehard RA: **Extracting patterns from large movement data sets using hybrid spatio-temporal filtering: A case study of geovisual analytics in support of fisheries enforcement activities.** *Master.* St. John's Newfoundland, Geography; 2012.

11. Van Moorter B, Visscher DR, Jerde CL, Frair JL, Merrill EH: **Identifying Movement States From Location Data Using Cluster Analysis.** *The Journal of Wildlife Management* 2010, **74:**588-594.

12. Gurarie E, Andrews RD, Laidre KL: **A novel method for identifying behavioural changes in animal movement data.** *Ecol Lett* 2009, **12:**395-408.

13. Thiebault A, Tremblay Y: **Splitting animal trajectories into fine-scale behaviorally consistent movement units: breaking points relate to external stimuli in a foraging seabird.** *Behav Ecol Sociobiol* 2013, **67:**1013-1026.

14. Allen A, Månsson J, Jarnemo A, Bunnefeld N: **The impacts of landscape structure on the winter movements and habitat selection of female red deer.** *European Journal of Wildlife Research* 2014, **60:**411-421.

15. Barraquand F, Benhamou S: **Animal movements in heterogeneous landscapes: identifying profitable places and homogeneous movement bouts.** *Ecology* 2008, **89:**3336-3348.

16. Nams VO: **Combining animal movements and behavioural data to detect behavioural states.** *Ecol Lett* 2014, **17:**1228-1237.

17. Morales JM, Ellner SP: **Scaling up animal movements in heterogeneous landscapes: the importance of behavior.** *Ecology* 2002, **83:**2240-2247.

18. Morales JM, Haydon DT, Frair J, Holsinger KE, Fryxell JM: **Extracting more out of relocation data: building movement models as mixtures of random walks.** *Ecology* 2004, **85:**2436-2445.

19. Patterson TA, Thomas L, Wilcox C, Ovaskainen O, Matthiopoulos J: **State-space models of individual animal movement.** *Trends Ecol Evol* 2008, **23:**87-94.

20. Dowd M, Joy R: **Estimating behavioral parameters in animal movement models using a state-augmented particle filter.** *Ecology* 2011, **92:**568-575.

21. Madon B, Hingrat Y: **Deciphering behavioral changes in animal movement with a 'multiple change point algorithm- classification tree' framework.** *Frontiers in Ecology and Evolution* 2014, **2**.

22. Bunnefeld N, Börger L, van Moorter B, Rolandsen CM, Dettki H, Solberg EJ, Ericsson G: **A model-driven approach to quantify migration patterns: individual, regional and yearly differences.** *J Anim Ecol* 2011, **80:**466-476.

23. Oswald SA, Nisbet ICT, Chiaradia A, Arnold JM: **FlexParamCurve: R package for flexible fitting of nonlinear parametric curves.** *Methods in Ecology and Evolution* 2012, **3:**1073-1077.

24. Borger L, Fryxell J: **Quantifying individual differences in dispersal using net squared displacement.** In *Dispersal Ecology and Evolution.* Edited by Clobert J, Baguette M, Benton TG, Bullock JM. Oxford, UK: Oxford University Press; 2012: 222-230

25. Gurarie E: **bcpa: Behavioral change point analysis of animal movement.** In *Book bcpa: Behavioral change point analysis of animal movement* (Editor ed.^eds.). City; 2013.

26. Turchin P: *Quantitative Analysis of Movement: Measuring and Modeling Population Redistribution in Animals and Plants.* Sunderland, Massachusets: Sinauer Associates Inc.; 1998.

27. Beatty WS, Kesler DC, Webb EB, Raedeke AH, Naylor LW, Humburg DD: **Quantitative and Qualitative Approaches to Identifying Migration Chronology in a Continental Migrant.** *PLoS ONE* 2013, **8:**e75673.

28. Mysterud A, Bischof R, Loe LE, Odden J, Linnell JDC: **Contrasting migration tendencies of sympatric red deer and roe deer suggest multiple causes of migration in ungulates.** *Ecosphere* 2012, **3:**art92.

29. Killeen J, Thurfjell H, Ciuti S, Paton D, Musiani M, Boyce M: **Habitat selection during ungulate dispersal and exploratory movement at broad and fine scale with implications for conservation management.** *Movement Ecology* 2014, **2:**15.

30. Curio E: *The ethology of predation.* Springer-Verlag; 1976.

31. Spitz F, Janeau G: **Spatial strategies: an attempt to classify daily movements of wild boar.** *Acta Theriologica* 1990, **35:**129-149.

32. Clobert J, Baguette M, Benton TG, Bullock JM, Ducatez S: *Dispersal Ecology and Evolution.* OUP Oxford; 2012.

33. Di Orio AP, Callas R, Schaefer RJ: **Performance of two GPS telemetry collars under different habitat conditions.** *Wildl Soc Bull* 2003, **31:**372-379.

34. Cavadini M: **Evaluation of the influence of topography and the structure of vegetation upon the success rate and the precision of the GPS-telemetry in the Palatinate Forest (Pfälzerwald, Südwestpfalz district, Germany).** HES Nature Management; 2007.

35. R Development Core Team: **R: A language and environment for statistical computing.** In *Book R: A language and environment for statistical computing* (Editor ed.^eds.). City: R Foundation for Statistical Computing; 2013.

36. Huang S, Meng SX, Yang Y: **Assessing the goodness of fit of forest models estimated by nonlinear mixed-model methods.** *Canadian Journal of Forest Research* 2009, **39:**2418-2436.

37. Ward JH: **Hierarchical Grouping to Optimize an Objective Function.** *Journal of the American Statistical Association* 1963, **58:**236-244.

38. Podgórski T, Baś G, Jędrzejewska B, Sönnichsen L, Śnieżko S, Jędrzejewski W, Okarma H: **Spatiotemporal behavioral plasticity of wild boar (*Sus scrofa*) under contrasting conditions of human pressure: primeval forest and metropolitan area.** *J Mammal* 2013, **94:**109-119.

39. Schley L, Roper TJ: **Diet of wild boar *Sus scrofa* in Western Europe, with particular reference to consumption of agricultural crops.** *Mamm Rev* 2003, **33:**43-56.

40. Keuling O, Stier N, Roth M: **Commuting, shifting or remaining? Different spatial usage patterns of wild boar *Sus scrofa* L. in forest and field crops during summer.** *Mammalian Biology* 2009, **74:**145-152.

41. McIlroy JC, Saillard RJ: **The effect of hunting with dogs on the numbers and movements of feral pigs, Sus scrofa, and the subsequent success of poisoning exercises in Namadgi National Park, ACT.** *Australian Wildlife Research* 1989, **16:**353-363.

42. Keuling O, Stier N, Roth M: **How does hunting influence activity and spatial usage in wild boar *Sus scrofa* L.?** *European Journal of Wildlife Research* 2008, **54:**729-737.

43. Bjorneraas K, Van Moorter B, Rolandsen CM, Herfindal I: **Screening Global Positioning System Location Data for Errors Using Animal Movement Characteristics.** *The Journal of Wildlife Management* 2010, **74:**1361-1366.

44. Tolon V, Dray S, Loison A, Zeileis A, Fischer C, Baubet E: **Responding to spatial and temporal variations in predation risk: space use of a game species in a changing landscape of fear.** *Canadian Journal of Zoology* 2009, **87:**1129-1137.

45. Gurarie E, Andrews RD, Laidre KL: **A novel method for identifying behavioural changes in animal movement data.** *Ecol Lett* 2009, **12:**395-408.

46. Hansson LA, Akesson S: *Animal Movement Across Scales.* Oxford, UK: Oxford University Press; 2014.

47. Russo L, Massei G, Genov PV: **Daily home range and activity of wild boar in a Mediterranean area free from hunting.** *Ethol Ecol Evol* 1997, **9:**287-294.

48. Spitz F, Janeau G: **Daily selection of habitat in wild boar (*Sus scrofa*).** *J Zool* 1995, **237:**423-434.

49. Janeau G, Cousse S, Cargnelutti B, Spitz F: **Role of daily movements in the socio-spatial organization of wild boar populations (*Sus scrofa* L.).** *Revue d'Ecologie (La Terre et la Vie)* 1995, **50:**35-48.

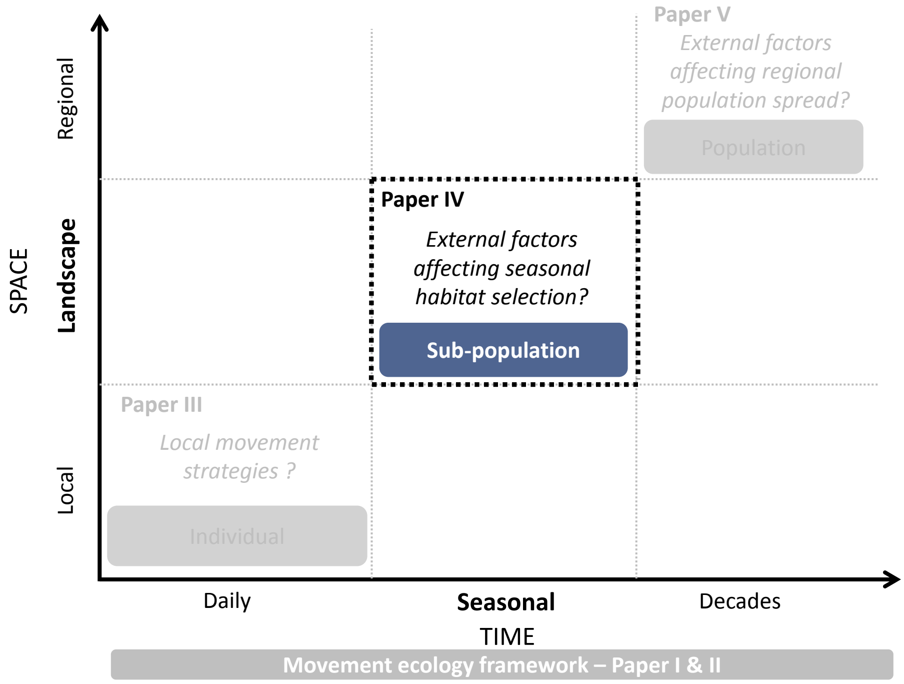
50. Suselbeek L, Adamczyk VMAP, Bongers F, Nolet BA, Prins HHT, van Wieren SE, Jansen PA: **Scatter hoarding and cache pilferage by superior competitors: an experiment with wild boar, Sus scrofa.** *Anim Behav* 2014, **96:**107-115.

51. Keuling O, Stier N, Roth M: **Commuting, shifting or remaining?. Different spatial utilisation patterns of wild boar *Sus scrofa* L. in forest and field crops during summer.** *Mammalian Biology* 2009, **74:**145-152.

Supplementary material - Table 1. Central tendency and variability (mean ± sd) for a range of descriptive statistics for each of the nine detected movement strategies.

Parameter	ID	Dispersal						Circular				Nomadic		Residency	
		Short		Medium		Long		Complete		Partial					
N trips	1	48		4		2		16		40		12		21	
	2	77		18		1		6		28		12		8	
	3	59		2		1		15		37		11		11	
		Mean	sd	Mean	sd	Mean	sd	Mean	sd	Mean	sd	Mean	sd	Mean	sd
Number of positions per segment	1	40.2	18.7	40.8	14.8	36		39.8	14.2	39.8	16.3	35.5	14.7	34.1	10.5
	2	39	16.1	39.1	14.4	32		36.7	8	47.3	31.8	43.4	15.6	41	19.6
	3	40.4	16.5	32	1.4	36		41.1	19	40.2	20.1	40.1	7.1	35.7	17.6
Total distance travelled (km)	1	3.1	1.4	5.4	0.5	8.9		4.4	2.4	3.4	2.1	3.4	2	1.2	0.7
	2	2.6	1.5	9.4	3.5	21.9		5	5.5	4.2	4.6	6.6	8.2	3.8	5.6
	3	3.8	3	8.5	1.1	11.7		4.1	2.9	4.4	2.7	4.5	4	2.5	2.4
Total segment time (hours)	1	10.8	5	10.7	4.7	8.7		10	3.5	10.6	4.6	9	3.8	8.8	2.6
	2	10.3	4.4	10.6	3.8	8.5		9.9	1.4	12.1	8	11.5	5	11.1	4.6
	3	10.3	4.3	7.9	0.2	9		10.3	4.7	10.3	5	10.2	2.1	9.4	4.6
speed (m/sec)	1	0.09	0.05	0.16	0.06	0.32		0.13	0.08	0.1	0.07	0.12	0.07	0.04	0.04
	2	0.08	0.05	0.29	0.13	0.76		0.13	0.12	0.11	0.11	0.19	0.23	0.08	0.08
	3	0.11	0.08	0.3	0.04	0.34		0.11	0.05	0.14	0.1	0.12	0.08	0.07	0.07
Final distance from origin (distEnd) (km)	1	1.4	0.6	3.1	0.3	5.5		0.4	0.4	1	0.6	1	0.7	0.1	0.1
	2	1.3	0.9	5.7	1.1	9.9		0.6	1	1.6	2	2.6	4.4	0.5	0.8
	3	1.8	1.1	5.9	0.6	8.5		0.4	0.3	1.5	1.1	1.6	1.5	0.4	0.3
Peak Distance (peakD) (km)	1	1.5	1.3	3.1	1.7	5.4		1.2	1.2	1.4	1.4	1.4	1.3	0.2	0.2
	2	1.6	1.7	5.7	3.3	9.1		2.7	3.8	2.8	4.4	4.9	8.4	1.2	1.8
	3	2	2.1	5.9	3	8.7		1.4	1.5	2.2	2.6	2.2	2.9	0.7	0.9
peakD/distEnd	1	1.1	2.1	1	6.1	1		2.9	3.2	1.4	2.3	1.3	1.8	2.4	2.3
	2	1.2	1.9	1	3.1	0.9		4.2	3.9	1.7	2.3	1.9	1.9	2.5	2.2
	3	1.2	2	1	5.4	1		3.7	5.1	1.5	2.2	1.4	1.9	2	2.6

A.4 PAPER IV



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ORIGINAL PAPER

Seasonal variations of wild boar *Sus scrofa* distribution in agricultural landscapes: a species distribution modelling approach

Kevin Morelle · Philippe Lejeune

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Abstract Seasonal changes in the distribution of animals can have an important impact on the ecosystem. In agricultural landscapes, the seasonal movement of the wild boar *Sus scrofa* towards field crops often results in damages and makes control of the population difficult. The plasticity of the species to cope with different habitats is largely proven, but the environmental and human drivers of this seasonal habitat shift at the population scale remain largely unknown. Using MaxEnt and two seasonally distinct presence datasets, we contrasted the distribution of wild boar in southern Belgium during the growing and hunting seasons to (i) analyse seasonal drivers of the distribution and (ii) forecast the potential spread of the species north to its current distribution. We demonstrated that during the growing season, wild boar range almost double, owing to the cover and food provided by agricultural areas, thereby enhancing the movement and spread of the species. We found that the seasonal distribution of wild boar in agricultural lands is mostly influenced by the search for cover and food provided alternatively by forest and field crops. Interestingly, it seems that this search for cover operates under the constraint of a threshold distance. Our results indeed reveal an increased probability of presence not only in the vicinity of forests but also above a threshold distance of 865 m from the forest edge, suggesting that wild boar can overcome the dependence to forest cover. The forecast distribution of wild boar highlighted a potential increase of the current range into suitable habitat between 63 and 168 km^2. To counteract the potential spread of the species into agricultural habitats and the consecutive damages, we insist on the need for the development of integrated management strategies, combining land use spatial configuration and wild boar spatial behaviour.

Keywords Growing season · Habitat shift · Hunting season · MaxEnt · Wallonia

Introduction

The facilities that the environment offers to animals, from food resources to thermal or safety cover, are continuously changing under human, climatic or weather constraints (Schloss et al. 2012; Sih et al. 2011). Therefore, animals have to develop strategies and adapt their space use with respect to these changes (Fryxell and Sinclair 1988). Understanding drivers and strategies developed by animals to cope with changing environments has become a challenging research topic in science (Winkler et al. 2014). To respond to environmental fluctuations, animals can either adapt their physiology, e.g. decrease the metabolic rate (Brinkmann et al. 2012) and change the daily activity rhythm (Cloudsley-Thompson 1966), or their spatial ecology (Birkett et al. 2012; Ramanzin et al. 2007), e.g. migrate at various distances to reach better environment (Mysterud 1999; Singh et al. 2012). The decision to change of habitat rarely involves only one cause but rather implies a trade-offs estimation between benefits and costs associated with habitat change (Brönmark et al. 2008). Though changing the habitat may increase the predation risk, e.g. while crossing a hostile matrix (Russell et al. 2003), migrating or shifting has usually in common to increase individual fitness, e.g. enhancing body conditions (Gaidet and Lecomte 2013), survival (Skov et al. 2013) or prolificy (Rosell et al. 2012).

Within its native Eurasian range, not only wild boar *Sus scrofa* population size has increased during these last decades but also it distribution area. The species has indeed expanded

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K. Morelle (✉) · P. Lejeune
BIOSE (Biosystem engineering), University of Liège - Gembloux Agro Bio Tech, passage des déportés 2, 5030 Gembloux, Belgium
e-mail: morelle.k@gmail.com

its distribution in the Northern Hemisphere, by re-colonizing Fenno-Scandinavian and Baltic territories (Erkinaro et al. 1982; Rosvold and Andersen 2008; Veeroja and Männil 2014), but has also gained areas in agricultural (Herrero et al. 2006; Keuling et al. 2009), mountainous (Baubet et al. 2004; Sarasa 2013) and peri-urban (Cahill and Llimona 2004; Cahill et al. 2012) environments. Owing to its diet (Schley and Roper 2003), spatial behaviour (Podgórski et al. 2013) and life strategy (Gamelon et al. 2013) plasticity, the species can indeed easily cope within these fluctuating environments. In wild boar, it seems that the strategy adopted to cope with seasonal changes is based on their movement abilities (Morelle et al. 2014). These movements are generally the consequence of variations in resource availability (Herrero et al. 2006; Keuling et al. 2009; Schley and Roper 2003; Singer et al. 1981), protection cover (Keuling et al. 2009) or predator avoidance (Tolon et al. 2009). From an evolutionary perspective, wild boar is a species that is well adapted to landscapes providing shelter, e.g. forest and its understorey (Briedermann 1990) or bushland in Mediterranean regions (Acevedo et al. 2006; Meriggi and Sacchi 2001). Since the development of modern agriculture by human at the expense of forest, together with wild boar domestication and consecutive interbreeding, wild boar could progressively adapt to agro-forested landscapes (Rosvold et al. 2010), e.g. enabling the species to take advantages of hedges and high crops as an alternative cover for their movement (Thurfjell et al. 2009). Use of agricultural crops by wild boar is thus probably not a recent fact but is rather concomitant to the development of agriculture by human, explaining why wild boar has now become so common in these agro-forested landscapes that cover 40 % of Europe (Estreguil et al. 2012). In these areas, use of field crops by wild boar generally induces damages that can result in important economic consequences and cause conflicting issues between hunters and farmers (Amici et al. 2012; Barrios-Garcia and Ballari 2012; Herrero et al. 2006; Schley et al. 2008). Shifting to agricultural environments during the growing season not only offers energetic advantages to wild boar (Rosell et al. 2012) but also provides a quiet environment, preserved from the numerous human activities observed in forests (Colson et al. 2010). After the growing season, when fields have been harvested, the main hunting season starts in most European countries (Apollonio et al. 2010) and wild boar return to forest areas. Thus, this change in resource availability and predation risk between the growing and the hunting season forces the wild boar to adapt its spatial behaviour (Keuling et al. 2009; Tolon et al. 2009). To date, little is known on the process and drivers of this habitat shift at the population scale and how the seasonal range of wild boar is affected.

The present paper aims to compare the distribution of wild boar during two contrasted seasons, the growing and the hunting season, and to forecast the potential distribution of wild boar in northern Wallonia where the species recently started to spread. We hypothesized that the seasonal adaptation of wild boar to changing environment should be reflected in a change of its distribution; therefore, we decided to take a species distribution modelling approach (Franklin and Miller 2009). The identification of distribution drivers and potential spread of wild boar is fundamental to inform in advance game managers and to develop effective management and control strategies in order to prevent agricultural damages (Saito et al. 2012). Therefore, the results of our study will be helpful for farmers and wildlife managers in order to identify target areas in which the management of the species is urgently required for avoiding coexistence issues. Such knowledge is particularly important because the propensity of the species to cause damages to crops and to spread into novel habitats greatly depends on this shifting ability.

Material and methods

Study area

Owing to a south–north gradient of transitional landscapes between forest and agriculture, Southern Belgium offers a particularly interesting context to study the behaviour of wild boar (Cellule Etat de l'environnement wallon 2010). The population initially bounded to large forest areas of Ardennes, progressively spread since the 1980s to the North (Prevot and Morelle 2012). We focused our analysis on the Condroz and Loamy regions, located in Wallonia, South of Belgium (Fig. 1a). These regions are separated by the presence of a long channel made by the Meuse and Sambre rivers. The channel partially acts as a natural barrier slowing down the spread of large animals northwards. South to the channel, in Condroz, the presence of wild boar is confirmed for more than 20 years, while North to the Channel, in the Loamy region, the presence of wild boar is more sporadic (Prevot and Morelle 2012). We built the species distribution models on presence data of wild boar from Condroz ecoregion and forecast the potential distribution in the Loamy region. The Condroz region occupies an area of 1,689 km^2, mainly comprising a mosaic of forests, pastures and agricultural lands, representing 29.5, 28.8 and 37.2 %, respectively, of the total area. The Loamy region covers 5,463 km^2 and is more agricultural, with 58.9 % of its area composed of field crops and 19.3 % of pastures, while forests constitute 9.6 % of the total area. The region is characterized by sub-oceanic climate with a mean annual temperature of 8 °C, 900 mm of mean annual rainfall and 25 days in average of snow cover. Elevation ranges from 50 to 350 m.a.s.l (Cellule Etat de l'environnement wallon 2010).

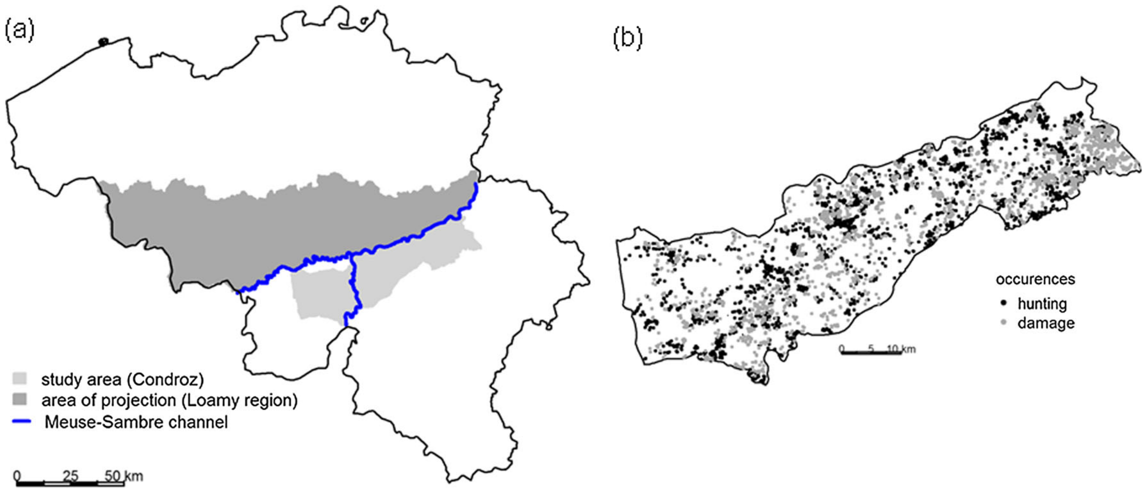


Fig. 1 **a** Location of the study area and the area of model projection; **b** distribution of hunting and damage occurrences in the study area

Wild boar occurrences

To model the wild boar distribution in southern Belgium, we adopted a presence-only method because it offers the opportunity to model the distribution of species without providing absence data, usually difficult to collect, and presenting uncertainty (Lobo et al. 2010). We used presence datasets covering different periods of the year, assuming they inform on the seasonal distribution and requirements of wild boar. We gathered occurrences from damages to agriculture, representing the growing season and covering the 1st of April to 30th of September period and from hunting bag records representing the hunting season, covering the 1st October to 31st December period.

Hunting bag records were collected from the five game management units (GMU) included in the study area. GMU are organized into hunting territories lead by game managers whom are responsible to report yearly hunting bag records. Although the participation of hunting territories to GMU is not mandatory in Wallonia, 382 hunting territories covering 82 % of the total study area . These hunting territories have a mean area of 2.5±2.0 km^2. As the exact location of the animal shot was not known but only the forest parcel, we applied non-point technique to generate occurrences (Koren et al. 2011). For each forest parcel, an equal number to the mean number of individuals shot in 2009 and 2010 was randomly generated within the boundary of the plot. We used the mean between two hunting seasons to avoid a potential bias due to higher or lower shooting due to unforeseen causes, e.g. harsh or mild winter conditions or particular local game management policies. We assumed that the method used was devoid of errors because the mean size of the forest parcel was of 8.8 ha and thus smaller than the chosen resolution of 9 ha (300×300 m cell size), and far under the 5 km location errors assessed by Graham et al. (2008) as influencing SDM performance. In total, 1,724 occurrences were generated to represent the distribution of wild boar during the hunting season (Fig. 1b).

Damage location records were obtained from annual administrative statistics reported by farmers. For each of their parcel, farmers can mention the presence of wild boar damage if more than 5 % of the total parcel area is affected. The location of the damages is then attributed to the centre of the parcel. As for the hunting occurrences, we considered damages occurring in 2009 and 2010, and those damages that occurred in the following crop type: maize *Zea mays* L., cereals *Triticum* spp. and rapeseed *Brassica napus* L. We restricted our analyses to these three crops because they are commonly cultivated in the region and provide cover and/or resources for wild boar. In 2009 and 2010, maize was harvested at the end of September, which ensured that there was no overlap with the hunting season. This results in a total of 1,967 occurrences, representing the distribution of wild boar during the growing season (Fig. 1b).

Predictors

To build up environmental and human-related variables, we used the 1:10,000 National Geographic Institute (NGI) vectorial map (source, SPW-DGARNE) and the farmer declaration form, containing the type of crop of each agricultural parcel. From these maps, we derived distance and density-based covariates expected to influence wild boar distribution. For distance-related variables, we rasterized the NGI vector map and calculated the distance to the edge of forest, agricultural and human features, and the perpendicular distance to linear features (roads and watercourses). In addition, for the density-related variables, we converted the two maps into a point pattern layer, with one point per hectare for polygonal features and one point per hundred of metre for linear features. From these point layers, we then calculated the relative density of each features. Topographic features, i.e. altitude, slope and aspect, were derived from a digital elevation model. All the layers created were set at a resolution of 300×300 m. We prepared these layers using R (R Core Team 2013) and the following packages: raster (Hijmans and van Etten 2013), spatstat (Baddeley and Turner 2005) and SDMTools (VanDerWal et al. 2014). We considered potential multicollinearity among our predictors using the Pearson's coefficient. This analysis did not reveal any relation >0.75 (Dormann et al. 2013). Therefore, all the variables were considered for the modelling step (Table 1).

Data analysis

We built models not only for each season but also for a combination of the two seasons that we named *all seasons*. We used MaxEnt, a machine-learning technique that requires only presence data (Elith et al. 2011; Phillips et al. 2006). MaxEnt estimates a probability distribution by finding the function that maximizes information entropy between the distribution of predictors in the whole study area, and the constraint imposed by the set of presence points. The result is a probability of occurrence assigned to each cell of the study area. In MaxEnt, the distribution of the values taken by the predictors in the study area is called 'background'. Background was set to 10,000 locations for all models. Models were fitted using k-fold cross-validation method (Fielding and Bell 1997). During the cross-validation process, presence dataset is randomly sampled, without replacement, and split into two independent datasets. The training data, representing 75 % of the occurrences, are used to calibrate the model and the test data, made of the 25 % left, allows to evaluate the model performance, i.e. its ability to discriminate among presence and absence (Phillips et al. 2006). We assessed model predictive performance using the area under the receiver operating characteristics curve (AUC), a threshold independent metric. AUC score close to 1 indicates model with good discriminatory abilities between suitable habitat and a random background sample, while AUC score of 0.5 indicates that the model prediction is as good as a random guess.

Sampling bias: systematic sampling, spatial filtering and bias grid

Recent studies have demonstrated the negative effect of sampling bias on model performance (Boria et al. 2014; Fourcade et al. 2014; Kramer-Schadt et al. 2013). To consider this issue in our analyses, we tested four methods accounting for bias in sampling: (1) systematic sampling, (2) filtering, (3) bias grid and (4) combination of bias grid and filtering. Systematic sampling helped in reducing partially spatial aggregation by randomly sampling one occurrence per single cell of 300×300 m (Fourcade et al. 2014). Through spatial filtering (Kramer-Schadt et al. 2013), we decreased the spatial aggregation for the second time by randomly selecting one occurrence in a buffer zone of 300 m. These two methods, though they have been proven to improve model quality, do not consider the absence or lack of sampling effort in part of the study area. Our presence datasets come from the sampling conducted in forest and agricultural areas and are thus clearly affected by sampling bias towards these two habitats. To consider this issue, we used bias grids (Elith et al. 2010), which are simple maps containing information on the sampling probability across the whole study area. We created two bias grids, one for the hunting season, with a sampling probability of 1 in forests and 0 outside, and one for the growing season, with sampling probability of 1 in agriculture habitat and 0 outside. We predicted that the models considering sampling bias should perform better than those that do not. We thus had a total of 12 models, three seasons (growing, hunting and all) times four sampling bias methods (systematic, filtering, bias grid, combined). For each model, 20 replicates were run to generate standard deviation values on our measures of model performances and response variables. MaxEnt analyses were run from R using the dismo package (Hijmans et al. 2013).

Seasonal distribution

To observe change in the seasonal distribution of wild boar, we compared the importance of each variable in the hunting and the growing model. We also used response curves to observe the relationship between the logistic predictions and the variables that contributed the most to the model. Finally, we compared the difference in range occupied between the two seasons by generating binary suitable/unsuitable maps with the maximum of the sum of specificity and sensitivity as threshold value.

Forecast distribution

To predict the potential distribution of wild boar in northern Wallonia, we used the best model of the hunting, growing and all season model, ranked according to their AUC value. From the continuous probability of occurrence, we derived binary suitable–unsuitable map by means of thresholding rules. We applied five threshold probability values above, which we considered the species as present, and under, the species as absent: (1) equal sensitivity and specificity (Fielding and Bell 1997), (2) maximum of the sum of training sensitivity and specificity (Manel et al. 2001), (3) maximum Cohen's kappa statistic (Beerling et al. 1995), (4) the balance training omission, predicted area and threshold value and (5) the equate entropy of thresholded and original distributions (these last two threshold being provided by MaxEnt). To assess which of these thresholds performs the best, we compared the overlap

Table 1 List of predictors used for modelling wild boar distribution

Variables		Definition	Model
Forest	Deciduous	Density in deciduous forest	Hunting, Growing, All Seasons
	Coniferous	Density in forest edge	Hunting, Growing, All Seasons
	DistForest	Distance to forest (deciduous and coniferous)	Growing, All Seasons
Agriculture	Maize	Density in maize fields, derived from a point pattern of 1 point/hectare	Hunting, Growing, All Seasons
	Cereals	Density in cereals fields, derived from a point pattern of 1 point/hectare	Hunting, Growing, All Seasons
	Cover	Density in other crop types providing cover (miscanthus, sunflowers, hemp, linen) derived from a point pattern of 1 point/hectare	Hunting, Growing, All Seasons
	Rapeseed	Density in rapeseed fields, derived from a point pattern of 1 point/hectare	Hunting, Growing, All Seasons
	Grassland	Density in permanent grasslands, derived from a point pattern of 1 point/hectare	Hunting, Growing, All Seasons
	DistCrop	Distance to crop areas providing cover (=all but grasslands)	Hunting, All Seasons
Human	Roads	Density of roads	Hunting, Growing, All Seasons
	DistRoads	Distance to road network	Hunting, Growing, All Seasons
	Human	Density in human features (towns, buildings, facilities)	Hunting, Growing, All Seasons
	DistHuman	Distance to human features	Hunting, Growing, AllSeasons
Hydrogaphy	Hydro	Density in water network, derived from a point pattern (1 point/100 m)	Hunting, Growing, All Seasons
	DistHydro	Distance to closest water network	Hunting, Growing, All Seasons
Topography	Elevation	Mean altitude, derived from a 30-m resolution digital elevation model	Hunting, Growing, All Seasons
	Slope	Mean slope, derived from a 30-m resolution digital elevation model	Hunting, Growing, All Seasons
	Aspect	Mean aspect, derived from a 30-m resolution digital elevation model	Hunting, Growing, All Seasons

Density function from spatstat package (R), SDMTools package

between the predicted binary map and the observed distribution map of areas where wild boar are already present, resulting from an independent survey conducted in 2010 in northern Wallonia (Prevot and Morelle 2012). To measure the overlap between the predicted and observed prediction, we used the similarity statistic *D* of Warren et al. (2008). *D* statistics value lies between 0 and 1, with a value of 1 revealing a perfect overlap and a value of 0 revealing an absence of overlap.

Results

In general, models gave low to good performances, ranging from AUC=0.655 to AUC=0.797. In two out of three cases, for the growing season (AUC=0.797±0.039) and all seasons (AUC= 0.791±0.023) models, the methods combining spatial filtering and bias grid gave much higher quantitative estimates of performance than those not considering sampling bias (Table 2). However, for the hunting season model, the methods considering the full dataset gave the best performance (AUC=0.767±0.029). Based on the test sets, the predictive ability of the three best models gave the following results: $\mathrm{AUC}_{\mathrm{test}}$ hunting=0.820, $\mathrm{AUC}_{\mathrm{test}}$ damages=0.812 and $\mathrm{AUC}_{\mathrm{test}}$ hunting + damages=0.851.

Seasonal distribution of wild boar

During the growing season, the variables that contribute the most to the model were the distance to forests (34.6 %) followed by the density in cereals (26.0 %), the density in rapeseed (12.6 %) and the road density (7.4 %). During the hunting season, the most contributing variables were the distance to crops (30.9 %), the density in coniferous (22.7 %) and in deciduous (13.4 %) forests and the road density (6.6 %) (Fig. 2). For the model combining the two seasons, distance to crops (60.5 %) and distance to forests (24.5 %) were the most contributing variables followed by the density in cereals (3.9 %), coniferous (2.4 %) and deciduous forest (1.9 %).

The analysis of the relationship between the distance to cover and the probability of presence showed that during the growing season, there was a decrease in the probability of presence with a minimum at 865 m from the forest edge,

Table 2 AUC±SD values of the different models for 20 replicates. Details between brackets are the number of occurrences used to train the model

	Model Growing season	 Hunting season	 All seasons
Full dataset	AUC=0.731±0.024 (*n*=1,967)	AUC=0.762±0.021 (*n*=1,724)	AUC=0.686±0.013 (*n*=3,692)
Systematic sampling	AUC=0.712±0.030 (*n*=1,334)	AUC=0.749±0.024 (*n*=1,328)	AUC=0.682±0.020 (*n*=2,579)
Spatial filtering	AUC=0.716±0.030 (*n*=864)	AUC=0.760±0.036 (*n*=858)	AUC=0.711±0.025 (*n*=1,332)
Bias grid	AUC=0.770±0.021 (*n*=1,334)	AUC=0.652±0.026 (*n*=1,328)	AUC=0.758±0.017 (*n*=2,579)
Spatial filtering + bias grid	AUC=0.788±0.042 (*n*=864)	AUC=0.672±0.040 (*n*=858)	AUC=0.795±0.024 (*n*=1,332)

followed by an increase of presence above this distance (Fig. 3). During the hunting season, we observed a similar but inverse pattern of increase and decrease in the probability of presence in relation to distance with crops (Fig. 3). Between the two seasons, suitable area for wild boar almost doubled with an estimated 488.9 km^2 during the hunting season to 798.8 km^2 during the growing season.

Forecast distribution

Based on the comparison of the thresholding methods and the similarity values obtained, we found that for the different models, different threshold gave the best similarity value with the independent presence survey (Table 3). In the case of the growing season model, the *maximal training sensitivity and specificity* method was the best; for the hunting model, we obtained the *equate entropy of threshold and original distributions* as the best, while for a combination of the hunting and growing models, *maximum kappa* was the best method (Fig. 4). We consequently used these three cut-off methods to transform the continuous logistic probability presence maps into binary predictive maps of wild boar distribution in the Loamy region (Fig. 5). According to each models, we obtained the following suitable area: 366 km^2 with the hunting season model, 395 km^2 with the growing season model and 471 km^2 with the all season model. At present, the range occupied by wild boar in the Loamy region is of 303 km^2 (Prevot and Morelle 2012), which means according to our prediction that the distribution of wild boar in the Loamy region could increase by 63 to 168 km^2.

Discussion

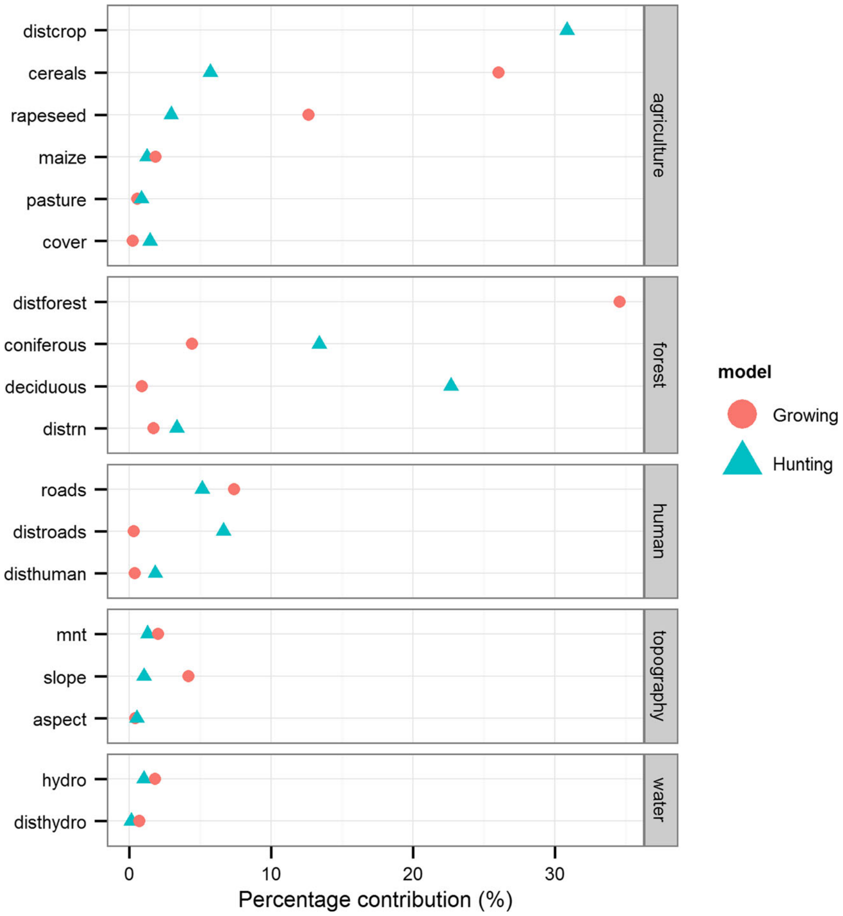
We have shown that wild boar population is able to spatially adjust its seasonal distribution in response to change in cover and food resources in agro-forested landscape, by increasing the use of agricultural areas during the growing season. This capacity of wild boar to face environmental fluctuations confirms the broad ecological niche of the species (Dardaillon 1986; Heinze et al. 2011; Podgórski et al. 2013; Schley and Roper 2003).

Seasonal redistribution

The distribution of the species seems to follow the seasonal availability of energy-rich food, mast and acorns in deciduous forests in winter and grains from field crops in summer (Ballari and Barrios-García 2013; Massei et al. 1996). In this sense, shifting in wild boar can be regarded as a behaviour following the optimal foraging strategy (MacArthur and Pianka 1966). This hypothesis seems to be confirmed by results from other studies, showing that when the forest offers high quality resources, naturally or artificially, agricultural areas are used with less intensity (Calenge et al. 2004; Meriggi and Sacchi 2001). However, artificial feeding effect on wild boar distribution remains unclear, and contradicting results have been obtained, in favour (Vassant 1994) or not (Hahn and Eisfeld 1998) of the ability of artificial food to keep wild boar in forests. However, the use by wild boar of agricultural areas prior to the grain maturation stages, period between the milky and the ripeness grain stage where crops can provide providential and substantial food resources for the wild boar (Schley et al. 2008), contradicts the optimal foraging strategy. Therefore, there may be additional explanations to the habitat shift observed in wild boar.

Landscape of fear generated by hunting activities has been shown to lead to habitat shift (Tolon et al. 2009). Although, we could not provide any map of the landscape of fear (van der Merwe and Brown 2008) to use as a predictor in the model, it is likely that in our study area, the predation risk created by hunting activities greatly influence wild boar spatial behaviour. In Wallonia, wild boar can be hunted by means of single hunt all year long and mainly performed at the edge between forest and crop field or by means of driven hunt in forest areas from the 1st of October to 31st of December. Moreover, with the increase in damages, driven hunt in crops (mainly maize) can now be authorized in some case. Altogether, these hunting activities create a landscape of fear that can alter wild boar spatial behaviour (Saïd et al. 2012; Sodeikat and Pohlmeyer 2007; Tolon et al. 2009). This high hunting pressure at the forest edges can indirectly favour a complete shift into crops or constraint animals to stay in forest in order to avoid risk of being shot. In the presence of nature reserve where hunting activities were forbidden, Tolon et al. (2009) showed that the

Fig. 2 Predictors' contribution (in %) for the growing and the hunting model



response of wild boar to temporal changes in risk was to shift home range within nature reserve boundaries. To some extent, our results support the idea that field crops offer to wild boar similar protective comfort than nature reserves.

The main contributing variables in explaining the presence of wild boar during the growing season were the distance to the forest and the density in cereals and rapeseed. It not only confirms the results of numerous studies where distance to the forest edge is the most important predictor of damages to crop (Calenge et al. 2004; Saito et al. 2012) but also the importance of crops like rapeseed, wheat and maize on wild boar distribution in agro-forested landscapes (Brook and van Beest 2014; Keuling et al. 2009). Though wild boar demonstrates abilities to cope with more open landscape, the proximity to forest cover remains a major requirement for this originally forests or bushes-dwellers species (Briedermann 1990; Rosvold et al. 2010). After crops harvesting and the beginning of the hunting season, we observed a return movement of wild boar towards forests as demonstrated by the decrease in probability presence in the crop fields. At this moment, the distance to crop and density in deciduous forest, providers of mast and acorns, become the major variables controlling wild boar distribution (Brook and van Beest 2014).

Interestingly, we found evidence that wild boar relation to forest and agricultural cover operates under a threshold distance response. The observed threshold of 865 m probably corresponds to a distance under which individuals stay in close relation with the forest habitat, and above which, it correspond to individuals realizing a complete shift to crop fields for a longer period or on the move to join a forest patch further away. This observation is consistent with previous research showing the existence of various strategies of habitat use among individuals of a wild boar population (Keuling et al. 2009; Tolon et al. 2009). Given that our analyses were based on data considering the population scale, we cannot conclude from our observations that the entire wild boar population migrates in crop fields during the growing season. However, we could demonstrate that along the year, changes in the landscape structure and composition created by agricultural cycle increase areas suitable for the wild boar and that seemingly part of the population makes use of this habitat. In consequence, seasonal habitat shift observed in wild boar is more likely to be viewed as a partial shift process (Chapman et al. 2011). Individual variation in the food/predation perception may explain why only part of the population shift (Keuling et al. 2009; Tolon et al. 2009); however, the observed

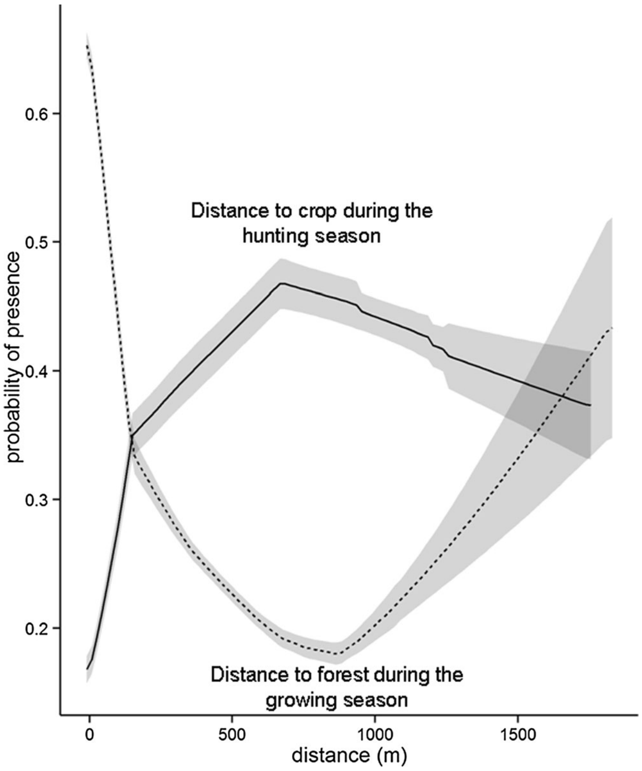


Fig. 3 Combined response curves of wild boar probability of presence in relation to crops during the hunting season (*full line*), and wild boar probability of presence in relation to forests during the growing season (*dashed line*)

shift could also be explained by a population strategy to decrease intraspecific competition in forest habitat as observed in other species. However, to confirm this hypothesis, more research studies on the share and the demographic structure of the population that perform these shift would be required (e.g. Martin et al. 2012). From the results obtained in this paper and according to the information available (Keuling et al. 2009), such study (e.g. based on telemetry, stomach content or isotopes analysis) would clearly help to understand consequences of habitat shift in terms of individual fitness and in terms of damage predictability.

Compared with others studies, we did not find an important effect of the proximity to water in explaining wild boar distribution (Choquenot et al. 1996; Meriggi and Sacchi 2001; Seo 2000). The important density in rivers and streams within the study area probably explain that access to water is not a limiting factor in Wallonia. Though the region is relatively flat, we expected that topographic variables, particularly the slope present along the river channel could have been expected to favour wild boar presence, owing to their relative quietness (Amici et al. 2012). We attribute the relative weak importance of these variables to the chosen resolution that does not reflect the potential use of these areas, rich in cover and hardly accessible for hunters, as highly suitable for the species.

We found that the habitat suitability of wild boar during the growing seasons almost doubled. This increase in suitability also promotes landscape connectivity for wild boar, i.e. facilitating movement within or along agricultural fields (Thurfjell et al. 2009). Thus, during the growing season, the agricultural matrix potentially constitutes an important corridor favouring wild boar exploration behaviour and enhancing population spread into novel habitats such as peri-urban and agricultural areas.

The present paper confirms the ability of MaxEnt to analyse seasonal changes in animal distribution (e.g. Suárez-Seoane et al. 2008) and to forecast distribution into novel areas (e.g. Verbruggen et al. 2013). Regarding model performances, the AUC values we obtained are in accordance with results from Saito et al. (2012) that predicted wild boar damage occurrences with MaxEnt. Moreover, our results support the idea that modelling the distribution of generalist species like wild boar results in a model with lower performance (Evangelista et al. 2008; Grenouillet et al. 2011). For specialist species having a small ecological niche, i.e. changes in distribution are easier to understand because the requirement of the species leads to a movement towards habitat offering the required resources. In contrast, for generalist species having a larger ecological niche, relating these habitat changes to requirements is more hazardous due to the their larger diet plasticity (Peers et al. 2012).

Table 3 Comparison of the binary projection for the three models with the independent observation survey. We considered the best threshold value as the one providing the best overlap with independent observation survey

Model	Best threshold	Threshold value	Area predicted (km^2)	*D* Warren statistic (overlap with observations from the 2010 survey)
Growing season	Maximal training sensitivity and specificity	0.389	366.8	0.970
Hunting season	Equate entropy of threshold and original distributions	0.195	395.6	0.976
All seasons	Kappa	0.543	471.2	0.985

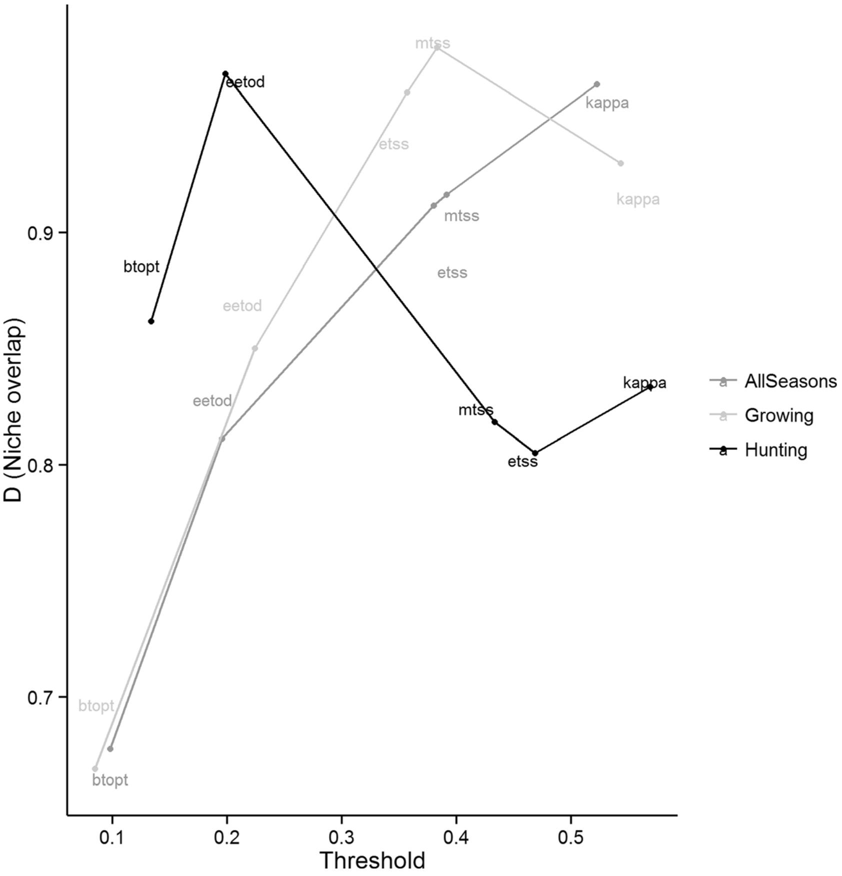


Fig. 4 Relationship between the five threshold measures and their effect on the overlap between the binary projection and the independent observation survey (*btopt*, balance training omission, predicted area and threshold value; *eetod*, equate entropy of thresholded and original distributions; *mtss*, maximal training sensitivity and specificity; *etss*, equate entropy of threshold and original distributions; *kappa* value at maximum kappa). *D* Warren statistic varies between 0 and 1, with 1 meaning perfect overlap and 0 absence of overlapping areas

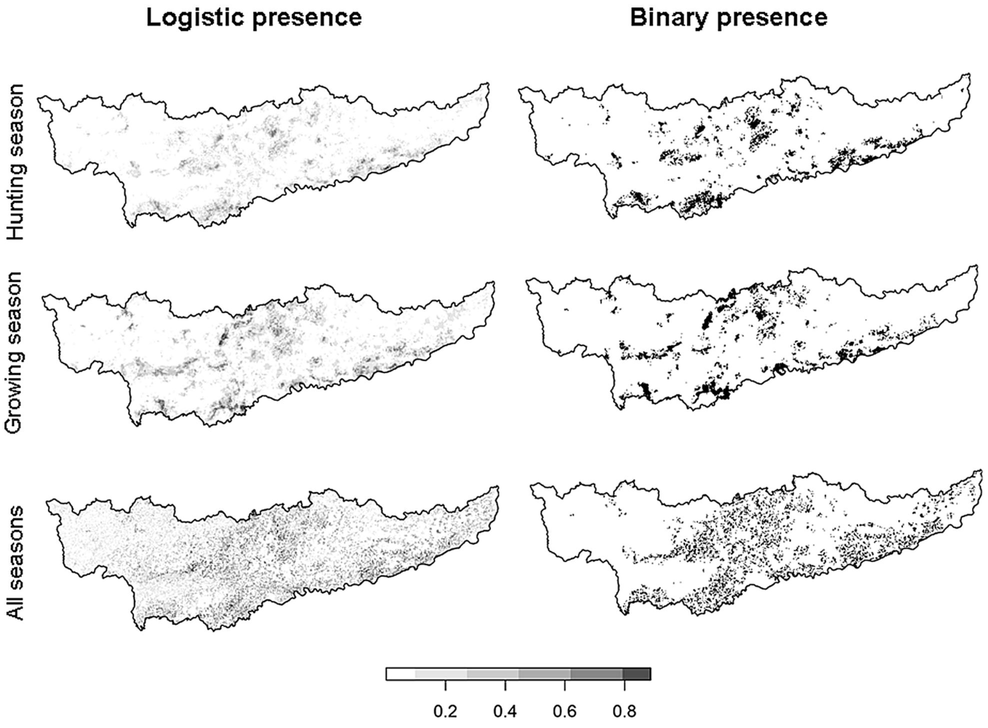


Fig. 5 Predictive map of the wild boar distribution in the Loamy region, logistic outputs *(left)* and binary outputs *(right)*

Sampling bias

By considering sampling bias in our analysis, we could partially confirm the finding from other studies, showing that considering sampling bias improves model performance (Boria et al. 2014; Fourcade et al. 2014; Kramer-Schadt et al. 2013). Apart from the hunting season model, we indeed found better performance when sampling bias was considered. According to our results, combining different methods such as filtering and bias grid improved model performance over the other methods (systematic sampling, filtering and bias grid). This result suggests that sampling bias should be overcome by combining multiple methods rather than using one method only. We explain the different result obtained from the hunting model by the fact that the distribution of the hunting points was less clustered than the damages points, hypothesis confirmed by a nearest neighbour exploratory analysis.

Management implications

In terms of habitat management, cultivating crops highly palatable to wild boar close to forest areas increases the risk of presence and damages of the wild boar (Calenge et al. 2004; Ficetola et al. 2014; Saito et al. 2012). However, our results tend to prove that avoiding the cultivation of such sensible crops close to the forest edges does not ensure a total absence of damages. Due to the ability of wild boar to move over long distances, encouraging the cultivation of these crops at a distance from the forest edges cannot be expected as a sufficient land use management measure. For a better understanding of the interaction between wild boar and agricultural lands, we encourage more studies relating agricultural landscape configuration and composition with wild boar movement abilities.

In terms of management of the species, our results clearly indicate a need to consider hunting not only in agricultural areas, which are close to the forest edge, but also to the parcel located farther and susceptible of being occupied by the species. It has been demonstrated that the absence or banning areas of hunting create a refuge effect favouring the risk of damages to crops (Amici et al. 2012). Therefore, an effort on the management and control strategies of wild boar in these landscapes should be promoted. Agro-forested areas seemingly require adapted methods, e.g. based on new technologies such as drone for animal detection (Chamoso et al. 2014) in crop fields, which could help hunters in their management activities.

In conclusion, the findings of this study confirm the ability of wild boar to adapt its distribution in highly dynamic landscape and suggest the importance of crop fields as alternative cover and food resources habitat for this species. By means of a comparative approach between seasonal distribution models, we have highlighted the shift in population distribution over two critical moments of the year for wild boar: the growing and the hunting seasons. In addition, the prediction in the North of Wallonia may help in allocating management efforts to locally and regionally restrict the expansion of the species.

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References

Acevedo P, Escudero MA, Muńoz R, Gortázar C (2006) Factors affecting wild boar abundance across an environmental gradient in Spain. Acta Theriol 51:327–336

Amici A, Serrani F, Rossi CM, Primi R (2012) Increase in crop damage caused by wild boar (*Sus scrofa* L.): the “refuge effect”. Agron Sustain Dev 32:683–692

Apollonio M, Andersen R, Putman RJ (2010) European ungulates and their management in the 21st century. Cambridge University Press, Cambridge

Baddeley A, Turner R (2005) Spatstat: an R package for analyzing spatial point patterns. J Stat Softw 12:1–42

Ballari SA, Barrios-García MN (2013) A review of wild boar *Sus scrofa* diet and factors affecting food selection in native and introduced ranges. Mammal Rev 44:124–134. doi:10.1111/mam.12015

Barrios-Garcia MN, Ballari SA (2012) Impact of wild boar (*Sus scrofa*) in its introduced and native range: a review. Biol Invasions 14:2283–2300

Baubet E, Bonenfant C, Brandt S (2004) Diet of the wild boar in the French Alps. Galemys 16:101–113

Beerling DJ, Huntley B, Bailey JP (1995) Climate and the distribution of *Fallopia japonica*: use of an introduced species to test the predictive capacity of response surfaces. J Veg Sci 6:269–282. doi:10.2307/3236222

Birkett PJ, Vanak AT, Muggeo VMR, Ferreira SM, Slotow R (2012) Animal perception of seasonal thresholds: changes in elephant movement in relation to rainfall patterns. PLoS ONE 7:e38363. doi:10.1371/journal.pone.0038363

Boria RA, Olson LE, Goodman SM, Anderson RP (2014) Spatial filtering to reduce sampling bias can improve the performance of ecological niche models. Ecol Model 275:73–77. doi:10.1016/j.ecolmodel.2013.12.012

Briedermann L (1990) Schwarzwild. VEB Deutscher Landwirtschaftsverlag, Berlin

Brinkmann L, Gerken M, Riek A (2012) Adaptation strategies to seasonal changes in environmental conditions of a domesticated horse breed, the Shetland pony (*Equus ferus caballus*). J Exp Biol 215:1061–1068

Brönmark C, Skov C, Brodersen J, Nilsson PA, Hansson L-A (2008) Seasonal migration determined by a trade-off between predator avoidance and growth. PLoS ONE 3:e1957. doi:10.1371/journal.pone.0001957

Brook RK, van Beest FM (2014) Feral wild boar distribution and perceptions of risk on the central Canadian prairies. Wildl Soc Bull 38: 486–494. doi:10.1002/wsb.424

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

Cahill S, Llimona F, Cabaneros L, Calomardo F (2012) Characteristics of wild boar (*Sus scrofa*) habituation to urban areas in the Collserola Natural Park (Barcelona) and comparison with other locations. Anim Biodivers Conserv 35:221–233

Calenge C, Maillard D, Fournier P, Fouque C (2004) Efficiency of spreading maize in the garrigues to reduce wild boar (*Sus scrofa*) damage to Mediterranean vineyards. Eur J Wildl Res 50:112–120. doi:10.1007/s10344-004-0047-y

Cellule Etat de l'environnement wallon (2010) Tableau de bord de l'environnement wallon 2010, Edition SPW-DGARNE-DEMNADEE (DG: C. Delbeuck) ISBN: 978-2-8056-0017-3

Chamoso P, Raveane W, Parra V, González A (2014) UAVs applied to the counting and monitoring of animals. In: Ramos C, Novais P, Nihan CE, Corchado Rodríguez JM (eds) Ambient intelligence—software and applications, vol 291. Advances in intelligent systems and computing. Springer, New York, pp 71–80. doi:10.1007/978-3-319-07596-9_8

Chapman BB, Brönmark C, Nilsson J-Å, Hansson L-A (2011) The ecology and evolution of partial migration. Oikos 120:1764–1775. doi:10.1111/j.1600-0706.2011.20131.x

Choquenot D, McIlroy J, Korn T (1996) Managing vertebrate pests: feral pigs. Australian Government Publishing Service, Canberra

Cloudsley-Thompson JL (1966) Seasonal changes in the daily rhythms of animals. Int J Biometeorol 10:119–125. doi:10.1007/bf01426857

Colson V, Garcia S, Rondeux J, Lejeune P (2010) Map and determinants of woodlands visiting in Wallonia. Urban For Urban Green 9:83–91. doi:10.1016/j.ufug.2009.04.002

Dardaillon M (1986) Seasonal variations in habitat selection and spatial distribution of wild boar (*Sus scrofa*) in the Camargue, Southern France. Behav Process 13:251–268

Dormann CF et al (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36:27–46

Elith J, Kearney M, Phillips S (2010) The art of modelling range-shifting species. Methods Ecol Evol 1:330–342. doi:10.1111/j.2041-210X.2010.00036.x

Elith J, Phillips SJ, Hastie T, Dudík M, Chee YE, Yates CJ (2011) A statistical explanation of MaxEnt for ecologists. Divers Distrib 17:43–57

Erkinaro E, Heikura K, Lindgren E, Pulliainen E, Sulkava S (1982) Occurrence and spread of the wild boar (*Sus scrofa*) in Eastern Fennoscandia. Memoranda 58:39–47

Estreguil C, Caudullo G, de Rigo D, San Miguel J (2012) Forest landscape in Europe: pattern, fragmentation and connectivity. Eur Comm, Luxemb. doi:10.2788/77842

Evangelista PH, Kumar S, Stohlgren TJ, Jarnevich CS, Crall AW, Norman Iii JB, Barnett DT (2008) Modelling invasion for a habitat generalist and a specialist plant species. Divers Distrib 14:808–817

Ficetola GF, Bonardi A, Mairota P, Leronni V, Padoa-Schioppa E (2014) Predicting wild boar damages to croplands in a mosaic of agricultural and natural areas. Curr Zool 60:170–179

Fielding AH, Bell JF (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. Environ Conserv 24:38–49. doi:10.1017/S0376892997000088

Fourcade Y, Engler JO, Rödder D, Secondi J (2014) Mapping species distributions with MaxEnt using a geographically biased sample of presence data: a performance assessment of methods for correcting sampling bias. PLoS ONE 9:e97122. doi:10.1371/journal.pone.0097122

Franklin J, Miller JA (2009) Mapping species distribution: spatial inference and prediction. Cambridge University Press, Cambridge

Fryxell JM, Sinclair AR (1988) Causes and consequences of migration by large herbivores. Trends Ecol Evol 3:237–241

Gaidet N, Lecomte P (2013) Benefits of migration in a partially-migratory tropical ungulate. BMC Ecol 13:1–14. doi:10.1186/1472-6785-13-36

Gamelon M, Douhard M, Baubet E, Gimenez O, Brandt S, Gaillard J-M (2013) Fluctuating food resources influence developmental plasticity in wild boar. Biol Lett 9: doi:10.1098/rsbl.2013.0419

Graham CH et al (2008) The influence of spatial errors in species occurrence data used in distribution models. J Appl Ecol 45:239–247

Grenouillet G, Buisson L, Casajus N, Lek S (2011) Ensemble modelling of species distribution: the effects of geographical and environmental ranges. Ecography 34:9–17. doi:10.1111/j.1600-0587.2010.06152.x

Hahn N, Eisfeld D (1998) Diet and habitat use of wild boar (*Sus scrofa*) in SW-Germany. Gibier Faune Sauvage 15:595–606

Heinze E et al (2011) Habitat use of large ungulates in northeastern Germany in relation to forest management. For Ecol Manag 261: 288–296

Herrero J, Garcia-Serrano A, Couto S, Ortuno VM, Garcia-Gonzales R (2006) Diet of wild boar *Sus scrofa* L. and crop damage in an intensive agroecosystem. Eur J Wildl Res 52:245–250

Hijmans RJ, van Etten J (2013) raster: Geographic data analysis and modeling. R package version 2.1-37

Hijmans RJ, Phillips S, Leathwick J, Elith J (2013) dismo: species distribution modeling. R package version 0.8-17

Keuling O, Stier N, Roth M (2009) Commuting, shifting or remaining?: different spatial utilisation patterns of wild boar *Sus scrofa* L. in forest and field crops during summer. Mamm Biol 74:145–152. doi:10.1016/j.mambio.2008.05.007

Koren M, Find'o S, Skuban M, Kajba M (2011) Habitat suitability modelling from non-point data. The case study of brown bear habitat in Slovakia. Ecol Inf 6:296–302

Kramer-Schadt S et al (2013) The importance of correcting for sampling bias in MaxEnt species distribution models. Divers Distrib 19:1366–1379. doi:10.1111/ddi.12096

Lobo JM, Jiménez-Valverde A, Hortal J (2010) The uncertain nature of absences and their importance in species distribution modelling. Ecography 33:103–114. doi:10.1111/j.1600-0587.2009.06039.x

MacArthur RH, Pianka ER (1966) On optimal use of a patchy environment. Am Nat 100:603–609

Manel S, Williams HC, Ormerod SJ (2001) Evaluating presence–absence models in ecology: the need to account for prevalence. J Appl Ecol 38:921–931. doi:10.1046/j.1365-2664.2001.00647.x

Martin AE, Hoover TM, Richardson JS (2012) Modeling the role of stage-structured agonistic interactions in ontogenetic habitat shifts. Behav Ecol. doi:10.1093/beheco/ars171

Massei G, Genov PV, Staines BW (1996) Diet, food availability and reproduction of wild boar in a Mediterranean coastal area. Acta Theriol 41:307–320

Meriggi A, Sacchi O (2001) Habitat requirements of wild boars in the northern Apennines (N Italy): a multi-level approach. Ital J Zool 68: 47–55

Morelle K, Podgorski T, Prevot C, Keuling O, Lehaire F, Lejeune P (2014) Towards understanding wild boar *Sus scrofa* movement: a synthetic movement ecology approach. Mammal Rev. doi:10.1111/mam.12028

Mysterud A (1999) Seasonal migration pattern and home range of roe deer (*Capreolus capreolus*) in an altitudinal gradient in southern Norway. J Zool (Lond) 247:479–486. doi:10.1111/j.1469-7998.1999.tb01011.x

Peers MJL, Thornton DH, Murray DL (2012) Reconsidering the specialist-generalist paradigm in niche breadth dynamics: resource gradient selection by Canada lynx and bobcat. PLoS ONE 7: e51488. doi:10.1371/journal.pone.0051488

Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distributions. Ecol Model 190:231–259

Podgórski T, Baś G, Jędrzejewska B, Sönnichsen L, Śnieżko S, Jędrzejewski W, Okarma H (2013) Spatiotemporal behavioral plasticity of wild boar (*Sus scrofa*) under contrasting conditions of human pressure: primeval forest and metropolitan area. J Mammal 94:109–119. doi:10.1644/12-mamm-a-038.1

Prevot C, Morelle K (2012) Potentiel de dispersion du sanglier et historique de la colonisation de la plaine agricole. For Wall 121: 35–42

R Core Team (2013) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Ramanzin M, Sturaro E, Zanon D (2007) Seasonal migration and home range of roe deer (*Capreolus capreolus*) in the Italian eastern Alps. Can J Zool 85:280–289. doi:10.1139/Z06-210

Rosell C, Navàs F, Romero S (2012) Reproduction of wild boar in a cropland and coastal wetland area: implications for management. Anim Biodivers Conserv 35:209–217

Rosvold J, Andersen R (2008) Wild boar in Norway—is climate a limiting factor? vol 1. Norges teknisk-naturvitenskapelige universitet, Trondheim

Rosvold J, Halley DJ, Hufthammer AK, Minagawa M, Andersen R (2010) The rise and fall of wild boar in a northern environment: evidence from stable isotopes and subfossil finds. The Holocene 20: 1113–1121

Russell RE, Swihart RK, Feng Z (2003) Population consequences of movement decisions in a patchy landscape. Oikos 103:142–152. doi:10.1034/j.1600-0706.2003.12418.x

Saïd S, Tolon V, Brandt S, Baubet E (2012) Sex effect on habitat selection in response to hunting disturbance: the study of wild boar. Eur J Wildl Res 58:107–115

Saito M, Momose H, Mihira T, Uematsu S (2012) Predicting the risk of wild boar damage to rice paddies using presence-only data in Chiba Prefecture, Japan. Int J Pest Manag 58:65–71

Sarasa M (2013) Intensive monitoring suggests population oscillations and migration in wild boar *Sus scrofa* in the Pyrenees. Anim Biodivers Conserv 36:1

Schley L, Roper TJ (2003) Diet of wild boar *Sus scrofa* in Western Europe, with particular reference to consumption of agricultural crops. Mammal Rev 33:43–56

Schley L, Dufrêne M, Krier K, Frantz AC (2008) Patterns of crop damage by wild boar (*Sus scrofa*) in Luxembourg over a 10-year period. Eur J Wildl Res 54:589–599

Schloss CA, Nuñez TA, Lawler JJ (2012) Dispersal will limit ability of mammals to track climate change in the Western Hemisphere. Proc Natl Acad Sci U S A. doi:10.1073/pnas.1116791109

Seo CW (2000) Wild boar (*Sus scrofa coreanus Heude*) habitat modelling using GIS and logistic regression. PhD Thesis, Seoul National University

Sih A, Ferrari MCO, Harris DJ (2011) Evolution and behavioural responses to human-induced rapid environmental change. Evol Appl 4:367–387. doi:10.1111/j.1752-4571.2010.00166.x

Singer FJ, Otto DK, Tipton AR, Hable CP (1981) Home ranges, movements, and habitat use of european wild boar in Tennessee. J Wildl Manag 45:343–353

Singh NJ, Börger L, Dettki H, Bunnefeld N, Ericsson G (2012) From migration to nomadism: movement variability in a northern ungulate across its latitudinal range. Ecol Appl 22:2007–2020. doi:10.1890/12-0245.1

Skov C et al. (2013) Migration confers survival benefits against avian predators for partially migratory freshwater fish. Biol Lett 9: doi:10.1098/rsbl.2012.1178

Sodeikat G, Pohlmeyer K (2007) Impact of drive hunts on daytime resting site areas of wild boar family groups (*Sus scrofa* L.). Wildl Biol Pract 3:28–38

Suárez-Seoane S, García de la Morena EL, Morales Prieto MB, Osborne PE, de Juana E (2008) Maximum entropy niche-based modelling of seasonal changes in little bustard (*Tetrax tetrax*) distribution. Ecol Model 219:17–29

Thurfjell H, Ball JP, Ahlen P-A, Kornacher P, Dettki H, Sjoberg K (2009) Habitat use and spatial patterns of wild boar *Sus scrofa* (L.): agricultural fields and edges. Eur J Wildl Res 55:517–523. doi:10.1007/s10344-009-0268-1

Tolon V, Dray S, Loison A, Zeileis A, Fischer C, Baubet E (2009) Responding to spatial and temporal variations in predation risk: space use of a game species in a changing landscape of fear. Can J Zool 87:1129–1137. doi:10.1139/z09-101

van der Merwe M, Brown JS (2008) Mapping the landscape of fear of the cape ground squirrel (*Xerus inauris*). J Mammal 89:1162–1169. doi:10.1644/08-mamm-a-035.1

VanDerWal J, Falconi L, Januchowski S, Shoo L, Storlie C (2014) SDMTools: Species Distribution Modelling Tools: tools for processing data associated with species distribution modelling exercises. R package version 1.1-20

Vassant J (1994) L'agrainage dissuasif: résultats d'expériences. Bull Mensuel l'ONC 191:101–105

Veeroja R, Männil P (2014) Population development and reproduction of wild boar (*Sus scrofa*) in Estonia. Wildl Biol Pract 10:17–21

Verbruggen H et al (2013) Improving transferability of introduced species' distribution models: new tools to forecast the spread of a highly invasive seaweed. PLoS ONE 8:e68337. doi:10.1371/journal.pone.0068337

Warren DL, Glor RE, Turelli M (2008) Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. Evolution 62:2868–2883. doi:10.1111/j.1558-5646.2008.00482.x

Winkler D et al (2014) Cues, strategies, and outcomes: how migrating vertebrates track environmental change. Mov Ecol 2:10. doi:10.1186/2051-3933-2-10

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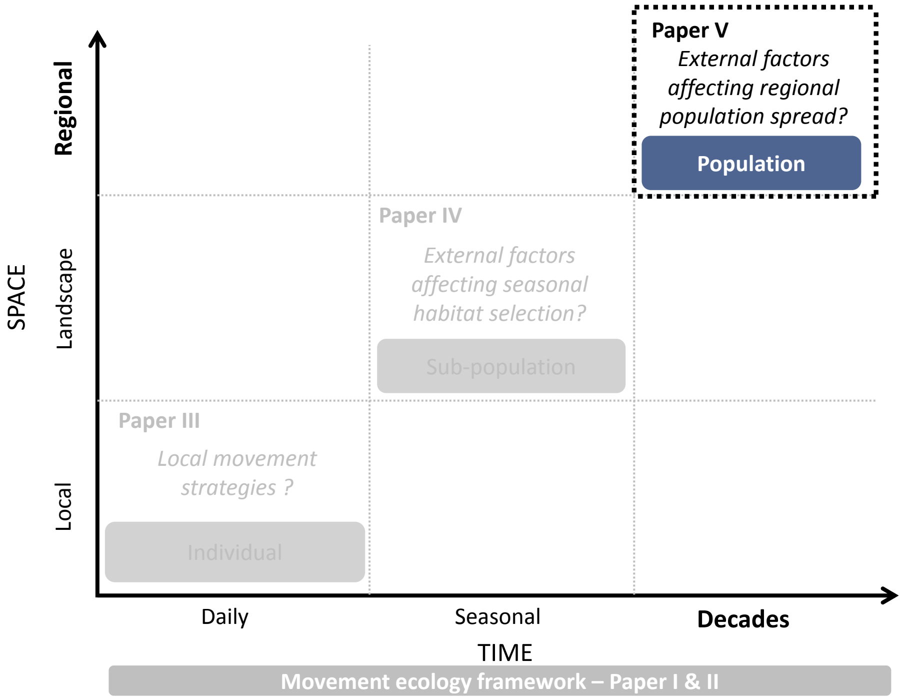

Morelle K, Fattebert J, Mengal C, Lejeune P Invasive in its native range: wild boar range expansion in European agro-landscapes. *Manuscript*

Invasive in its native range: wild boar range expansion in a European agro-landscape

Kevin Morelle[1*], Julien Fattebert[2], Coralie Mengal[1] and Philippe Lejeune[1]

[1] Gembloux Agro-Bio Tech, University of Liège, Department of Biosystem Engineering (BIOSE), Passage des Déportés 2, 5030 Gembloux, Belgium

[2] School of Life Sciences, Westville Campus, University of Kwazulu-Natal, 4000, Durban, South Africa

*Corresponding author:

Email: morelle.k@gmail.com

Phone: +32 (0)81 62.22.94

Fax: +32 (0)81 62.23.01

Abstract

Because native species can also expand their range with invasive-like patterns and consequences, detecting and understanding range expansion of native species is essential to improving management strategies. In this study, we documented the range expansion of a native invader, using wild boar *Sus scrofa* population recolonization of former range in southern Belgium as a biological model. We investigated the drivers of spatio-temporal change in wild boar distribution by means of four hypotheses (landscape, climate change, human-modified environment and the lack of control hypothesis). Over the last three decades, the distribution range of wild boar expanded northward into agricultural landscapes. This expansion was characterised by an exponential pattern of spread and a mean marginal velocity of 5 km year^{-1}. We showed that this expansion was mostly a density-dependent process driven by neighbouring population density, supporting the 'lack of control' hypothesis. Contrastingly, we found no support for the 'human modified environment' hypothesis, as increased area of cultivations providing cover (maize, rapeseed, cereals) did not facilitate wild boar range expansion. Moreover, colonization of wild boar was mostly promoted by forest habitat, showing the dominant role of this habitat in the population movement of this species. This study highlights the unforeseen consequence of the lack of population control of native invaders that leads to rapid recolonization of species' former range. Expansion of wild boar into agroecosystem has harmful impact and suggests that management plan for this species should keep the population density at levels that prevent population spread.

Keywords: native invader, population spread, Sus *scrofa*

Introduction

Though biological invasion is a well-recognized phenomenon, there is still no general agreement on its exact definition, so that cases of increase range expansion of native species remains poorly considered (Valéry et al. 2013, Valéry et al. 2008, Valéry et al. 2009). Indeed, most commonly animals and plants are considered as invasive only if they fulfill three conditions: i) they must be voluntary (Long 2003) or involuntary (Seebens et al. 2013) introduced by humans in novel environment (Perrings et al. 2010), ii) able to establish and spread (Jeschke and Strayer 2005) and iii) have a negative impact (Gurevitch and Padilla 2004, Heather and Dukes 2007, Olson 2006). However, a novel mechanistic definition based on the nature of the phenomenon itself was recently proposed, suggesting that biological invasion arises from species "acquiring a competitive advantage following the disappearance of natural obstacles to its proliferation, which allows it to spread rapidly and to conquer novel areas within recipient ecosystems in which it becomes a dominant population" (Valéry et al. 2008). With this new definition, range expansion of native species can be considered as biological invasion and under these circumstances being termed native invasive species (Valéry et al. 2009) or native invaders (Simberloff and Rejmanek 2010).

According to this new definition, biological invasion arises from the following causes: climate change, under-predation, and human-mediated expansion (Carey et al. 2012, Valéry et al. 2008). Climate-driven range shifts usually occur as a response to rising temperatures (Thomas et al. 2001). Absence or lack of predators prevent efficient population control which consequently growth when conditions are favourable and can further expand, e.g. density-dependent dispersal following demographic recovery enabling re-colonization of former range by locally or regionally extirpated species (Carey et al. 2012). Human-mediated expansion can occurs either directly via (re)-introduction of individuals (Acevedo and Cassinello 2009) or indirectly through changes brought to the environment favouring population increase and spread (Buczkowski 2010). Landscape heterogeneity and features that can either constitute a barriers hampering dispersal or a corridor connecting habitats promoting dispersal can affect movement and spread (With 2002). When conditions are favorable, native species can also display invasive-like traits. However, range expansion pattern of native species remains largely undocumented and consequently poorly understood (Carey et al. 2012, Valéry et al. 2009). Identification of causes leading a species to become invasive in its native range is however central to the understanding of species response to human- and natural-induced changes and the design of mitigation strategies, including dealing with over-abundance (Cromsigt et al. 2013, Gortázar et al. 2006).

In this study we investigated the patterns and drivers of native invader's range expansion. To this aim, we considered rapid range expansion as the invasive pattern to be observed and wild boar *Sus scrofa* as our biological model. We firstly documented and characterized the spatio-temporal patterns of wild boar expansion over the last three decades in southern Belgium, using information on historical patterns of distribution. Secondly, we modeled for each expansion phase the probability of unoccupied landscape units to be colonized as a response to the climatic, land use change, lack of population control or landscape hypothesis.

Material and Methods

Biological model

Among mammals, wild boar *Sus scrofa* is considered as one of the most invasive species in the world out of its native range (Lowe et al. 2004). Not only in its invasive range but also in its native range, wild boar has harmful ecological and socio-economical impact (Massei and Genov 2004, Putman et al. 2011). In Eurasia, the species has indeed expanded over the last three decades at the margin of its native Eurasian range (Erkinaro et al. 1982, Rosvold and Andersen 2008, Veeroja and Männil 2014), to such extent that the terms 'invasion' was even used to characterised this increase in its north eastern margin of the species' distribution (Danilkin 2001).

There are various mechanisms that have promoted the species to become a native invader: human-mediated environmental change, e.g. increased favourable cultivations (Geisser and Reyer 2005, Rosell et al. 2012), supplemental feeding or intentional stocking (Frantz et al. 2013), milder winter conditions and a relative decrease in the European hunters populations (Massei et al. 2014). Also, recent studies confirmed that wild boar holds many invasive traits leading to successful invasions (Jeschke and Strayer 2006): early age at first reproduction (Servanty et al. 2009), high reproductive output (Servanty et al. 2009), generalist feeding strategy (Schley and Roper 2003), spatial behavioral plasticity (Podgórski et al. 2013), and commensalism with humans (Cahill et al. 2012). Consequently this species can easily be regarded as a native invader. We used wild boar as a study case since the species recovery in terms of population size in its native Eurasian range has been acknowledged for decades (Saez-Royuela and Telleria 1986) but of which the spatial recovery, e.g. processes and mechanisms of range expansion favoring the species spread into new areas, remain largely unaddressed.

In Belgium, discovery of wild boar bone remains up to the North sea attest to the historical presence of the species over the entire territory of Belgium until the Middle age (Toussaint et al. 2011). Between AD 1500 and AD 1850, forest clearance for the development of agriculture range together with population increase and hunting pressure restricted the range of many forest-dwelling species in Europe (Kaplan et al. 2009). The wild boar consequently disappeared in many parts of its native range (Danilov and Panchenko 2012) and in Belgium its distribution decreased to the south until the highland Ardenne forest. Until the mid 20th century, the population remained in this area but since the 1980 progressively started to expand Northwards.

Study area

We focused our study on wild boar range expansion from Ardenne area to the North. This area encompasses four natural regions, from south to north: Ardennes, Fagne-Famenne, Condroz and Loamy regions (50°25’N, 4°53’E). These regions offer a north-south gradient in forest and agriculture cover from highly forest in the southern Ardenne region to highly agricultural in the Northern Loamy region (SPW 2012). The Meuse and Sambre rivers channel divides the study area and is a potential barrier to northward expansion on wild boar (Fig. 1). The area is characterized by sub-oceanic climate with mean annual temperature of 8°C, 900 mm of mean annual rainfall and 25 days snow cover in average. Elevation ranges from 50 to 350 m.a.s.l.

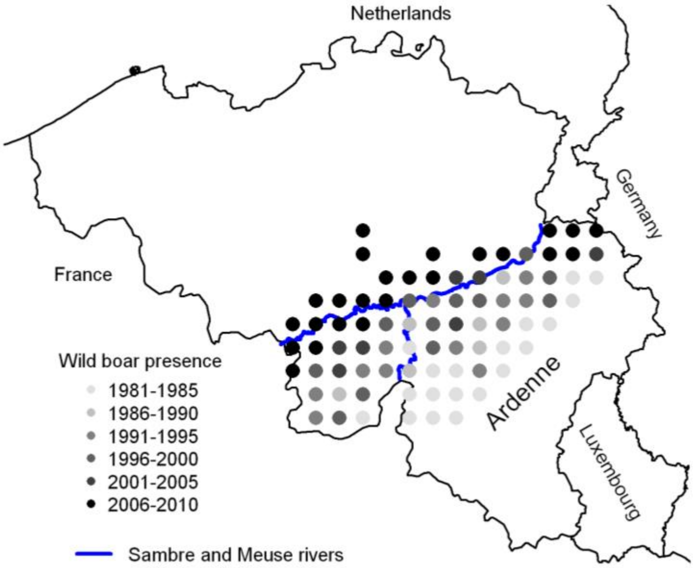

Fig. 1 Distribution map in 10x10-km grid of wild boar expansion, Wallonia, Belgium, 1981-2010.

Data sources

Period of colonization

We used a survey approach to document the expansion of wild boar range in our study area. We questioned game managers about dates of first appearance, first animal shot and permanent settling within their hunting territory. We assumed hunters would recall about wild boar status in their hunting ground within 5-year time windows and used this value as our temporal time step. For each time window, survey information was geo-referenced into a 10x10 km grid, so that a map of the spatio-temporal changes in wild boar distribution could be built (Fig. 1). Our grid resolution is consistent with the fact that >96% individuals have natal dispersal distance <10 km (Keuling et al. 2010, Prevot and Licoppe 2013). We only considered the earliest period of wild boar presence reported when different periods were recorded among several game units overlapping a same 10x10 km grid cell.

Colonization predictors

We use a total of eleven variables to explore the effect (positive or negative) of the four hypotheses on the colonization process of wild boar (Table 1). For all distinct period of wild boar colonization, we calculated the value of these variables at the 10x10 km grid scale as the average values over the five years.

Table 1. Independent variables used for modelling the colonization of wild boar.

Variables names	Description	Unit
Agricultural variables		
agriland	Area of grid covered by agriculture crops	km²
grass	Area of grid covered by grassland	km²
agricover	Mean area over the 5 considered years of the following crop type: maize *Zea mays,* rapeseed *Brassica napus,* cereals *Triticum spp.*	km²
Landscape variables		
forest	Area of grid covered by forest	km²
human	Area of grid covered by human building (villages, town, cities)	km²
road	Length of roads in each grid	km
rivers	Length of river in each grid	km
Population variables		
ndens	Mean neighbouring population density in the west, south-west, south, south-east and east neighbouring grids	Animal shot/100km²
Climatic variables		
tmean	Mean annual temperature	°C
tcold	Mean temperature of the coldest month	°C
twarm	Mean temperature of the warmest month	°C

The lack of control hypothesis corresponds to the absence of natural predators (Commission 2012) and the relative decrease numbers of hunters (Massei et al. 2014) combined to the poor efficiency of current hunting strategies (Cromsigt et al. 2013, Keuling et al. 2013). To measure the role of a lack of population control we used the ‘neighbouring population density’ variables, which the mean value of shot wild boar in the neighbouring occupied grids. Hunting statistics obtained from the Walloon Public Service were used to calculate this variable. We predicted that increase in population size favored wild boar expansion.

The human-modified landscape hypothesis corresponds to the agricultural components of the landscape. Here we considered three different components: grasslands, agricultural lands and agricultural cover. Grasslands correspond to the permanent grasslands area, mostly devoted to livestock. Agricultural lands (‘agriland’) correspond to all type cultivations. These two variables, grassland and agriland, were extracted from the Belgium National Geographic Institute (NGI) vector map. The third component, agricultural cover, corresponds to the cultivations providing shelter for the wild boar, i.e. maize *Zea mays*, rapeseed *Brassica napus* and cereals *Brassica spp.*. These crops are known to offer cover and/or resources to wild boar and we predicted that they would influence colonization of wild boar. Information on parcel cultivation was extracted from We built this variable (‘agricover’) by extracting and aggregating information at retrieved from the federal statistic (SPF Economie) for the period 1980-2000 and from the Walloon Public Service (SPW - SIGEC ‘Système Intégré de Gestion et de Contrôle’ – Agricultural land management map of Wallonia) for the period 1980-2010. We predicted that the increase surface of cultivations offering shelter favored population expansion.

Climatic change hypothesis relates to the increase in mean annual temperature (Ipcc 2014). To account for the effect of climatic change, we calculated for each grid over the 5-year period cover three variables: the mean annual temperature, the mean temperature of the coldest month and the mean temperature of the warmest month. We predicted that warming temperature would favor wild boar expansion.

The landscape hypothesis included habitat features putatively influencing occupancy positively (forest, rivers network) or negatively (transport infrastructures). Forest cover variable was extracted from the Belgium National Geographic Institute (NGI) vector map. Linear features (roads and rivers) are also known to influence wild boar movement, respectively slowing down (Frantz et al. 2012) and facilitating (Park and Lee 2003). For these two variables, we calculated from the 1:10 000 NGI vector map their overall length within each grid.

Data analysis

Range expansion pattern

To characterize the colonization process, we assumed a concentric population spread (Skellam 1951) and we calculated the radial range expansion as the square root of the area occupied at each period divided by π (Shigesada and Kawasaki 1997). We then a linear, a quadratic and an exponential regression to test the pattern of radial expansion range over time (Shigesada and Kawasaki 1997). Finally, by dividing the slope of this curve by the square root of π, we estimated the marginal velocity of range expansion for each period considered (Lensink 1997, Preuss et al. 2014).

Range expansion model

We firstly screened predictors for multicollinearity using a threshold of $|r|=0.7$ (Dormann et al. 2012). Variables that were highly correlated were: human buildings and roads, agriland and agricover and finally the three climatic variables. We retained human buildings because it is potentially attractive habitat for wild boar (Cahill et al. 2012). We also kept for further analysis the agricover variables because it was central to our hypothesis testing and known to influence wild boar distribution and dynamics (Brook and van Beest 2014, Geisser and Reyer 2005) and the mean annual temperature in our analysis because this variable is commonly used to track animal range-shift under climatic change (Chen et al. 2011).

We built a set of a priori candidate models to explore the contribution of the four hypotheses on the range expansion of wild boar (Table 2). Specifically, we modelled the probability of an empty grid to be colonized for each considered time period (1981-1985, 1986-1990, 1991-1995, 1996-2000, 2001-2005, 2006-2010) by means of a multivariate auto-logistic regression model (Silva et al. 2002). We used AIC model selection criteria corrected for small sample size (AICc) to select for most parsimonious models (Burnham and Anderson 2002). When candidate models were within ΔAICc < 2, we performed model averaging to estimate unbiased coefficients of the parameters. To identify informative parameters in final models, coefficients were deemed significant when corresponding 95% confidence interval (CI) did not include 0. All analyses were run in R 3.0.1 (R Core Team 2013).

Table 2. Hypothesis tested and related model structure.

Model no.	Hypothesis	Model structure
0	Null	ß0
1	Landscape	ß0 + ß1(landscape)
2	Population	ß0 + ß1(population)
3	Agriculture	ß0 + ß1(agriculture)
4	Climate	ß0 + ß1(climate)
5	Landscape, population	ß0 + ß1(landscape) + ß2(population)
6	Landscape, agriculture	ß0 + ß1(landscape) + ß2(agriculture)
7	Landscape, climate	ß0 + ß1(landscape) + ß2(climate)
8	Population, agriculture	ß0 + ß1(population) + ß2(agriculture)
9	Population, climate	ß0 + ß1(population) + ß2(climate)
10	Agriculture, climate	ß0 + ß1(agriculture) + ß2(climate)
11	Landscape, population, agriculture	ß0 + ß1(landscape) + ß2(population) + ß3(agriculture)
12	Landscape, population, climate	ß0 + ß1(landscape) + ß2(population) + ß3(climate)
13	Landscape, agriculture, climate	ß0 + ß1(landscape) + ß2(agriculture) + ß3(climate)
14	Population, agriculture, climate	ß0 + ß1(population) + ß2(agriculture) + ß3(climate)
15	Full	ß0 + ß1(landscape) + ß2(population) + ß3(agriculture) + ß4(climate)

Results

Range expansion pattern

Over the studied period, we observed a gradual spread of the wild boar margins' range, characterized by a continuous radial expansion (Fig. 2). This continuous expansion could be fitted by linear, exponential and quadratic regression.

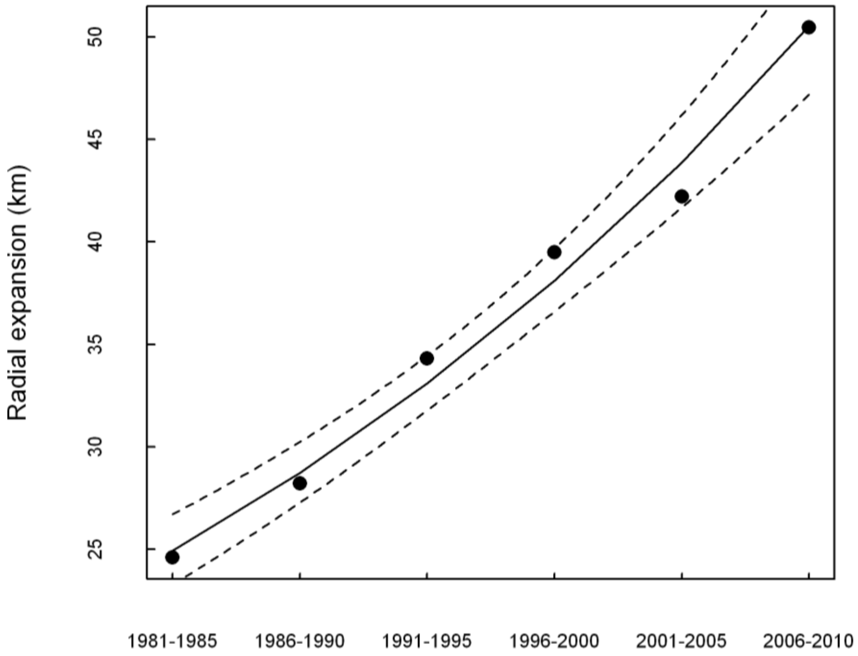

Fig. 2 Evolution of the radial expansion of wild boar in Wallonia, Belgium, 1981-2010.

We observed no statistical difference among the three regressions tested, however the exponential regression ($\beta=3.075$, SE=0.032, $p<0.0001$, $r^2=0.984$) gave a slightly better adjustment than the linear ($p<0.0001$, $r^2=0.982$) and the quadratic ($p=0.001$, $r^2=0.980$) regressions to explain radial range expansion over time.

During the studied period, the mean marginal velocity proceeded at a rate of 5.04 km year^{-1}. Temporal analysis of velocity period per period showed phases of acceleration and deceleration during the wild boar expansion process (Fig. 3): (i) until 1990 the speed of expansion was low; (ii) then it increased during until the year 2000, followed by (iii) important decrease in speed during the early 2000 and (iv) and finally a marked increase in velocity between 2006 and 2010 (Fig. 3).

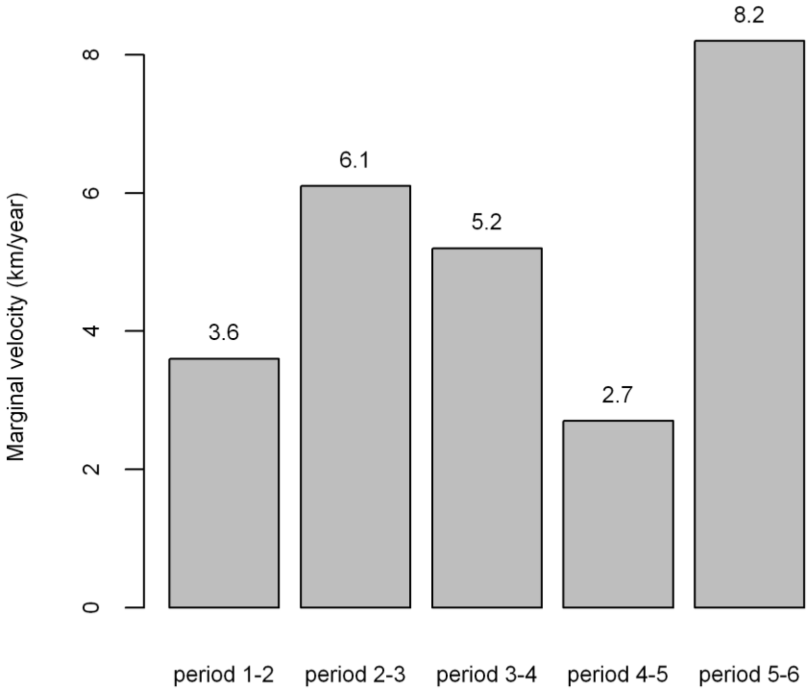

Fig. 3 Temporal variation in the observed marginal velocity.

Range expansion model

During the 1981-1985 period, the final averaged model highlighted two variables with a strong effect: cultivations providing cover that was negatively correlated with probability of colonization (agricover, β= 0.20, CI_{lower}-CI_{upper}=(-0.50,-0.010), fig.4b) and the neighbouring population density that was positively correlated (ndens, β= 0.05, CI_{lower}-CI_{upper}=(0.03, 0.20), fig.4a) (Table 3). In supplementary material Appendix 1 Table A1, we provide detailed results of the model selection for all colonization periods.

Table 3. Coefficient of the variables retained by the models averaging method along the different colonization phases of wild boar in Wallonia, Belgium. Bold indicates values that affect significantly the process of colonization.

Period	1981-1985		1986-1990		1991-1995		1996-2000		2001-2005		2006-2010	
	β	SE	β	SE	β	SE	β	SE	β	SE	β	SE
Forest	0.073	0.054	0.057	0.045	**0.095**	0.033	**0.196**	0.069	**0.215**	0.072	0.024	0.04
Rivers	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
Roads	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
Agricover	**-0.164**	0.162	**-0.055**	0.09	-	-	-	-	-	-	-0.011	0.033
Grasslands	-0.145	0.045	-0.022	0.039	-	-	-	-	-	-	0.072	0.083
ndens	**0.122**	0.049	**0.059**	0.039	**0.070**	0.028	**0.088**	0.037	**0.077**	0.039	0.037	0.042
tmean	-	-	-1.272	1.313	0.188	0.671	-0.345	1.129	-0.336	1.111	-1.055	1.869

In 1986-1990, three models, 5, 14 and the 7 had DAIC < 2. The two same variables (agricover, β= -0.06, CI$_{lower}$-CI$_{upper}$=(-0.30, -0.06), fig.4d and ndens, β= 0.06, CI$_{lower}$-CI$_{upper}$=(0.01, 0.10), fig.4c) had a significant effect on the colonization probability.

During the next colonization period, 1991-1995, the model 5 and the model 12 were the two best models, and the model averaging showed that the forest (forest, β= 0.10, CI$_{lower}$-CI$_{upper}$=(0.03, 0.16), fig.4f) and the neighbouring density (ndens, β= 0.07, CI$_{lower}$-CI$_{upper}$=(0.01, 0.12), fig.4e) variables were two significant and positively correlated variables with the colonization probability.

During the following two periods, between 1996 and 2005, we observed a similar scenario as n the previous colonization period, with models 5 and 12 being under DAIC < 2 and the probability of colonization of empty grids by wild boar being influenced by the forest (1996-2000, β= 0.20, C$_{lower}$-C$_{upper}$=(0.06, 0.33), fig.4h, and 2001-2005, β= 0.21, C$_{lower}$-C$_{upper}$=(0.06, 0.34), fig.4j) and the neighbouring population density (1996-2000, β= 0.09, C$_{lower}$-C$_{upper}$=(0.01, 0.16), fig.4g, and 2001-2005, β= 0.08, C$_{lower}$-C$_{upper}$=(0.01,0.17), fig.4i). During the last colonization period, models 8, 5 and 10 but no variables had a significant influence on the colonization process.

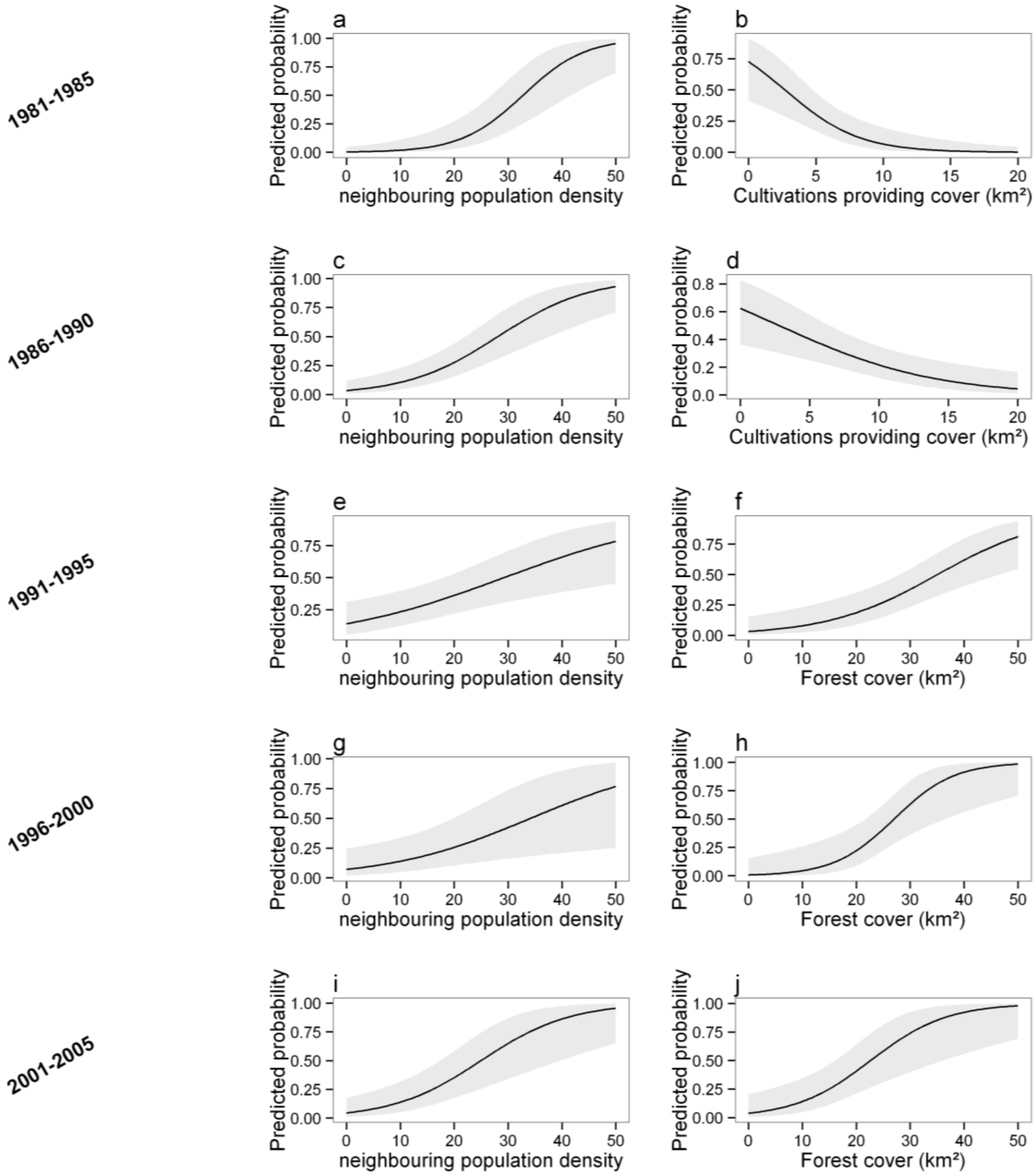

Fig. 4 a-j Variables with significant relationships with wild boar colonization probability for the different period of time considered.

During this northward range increase, we observed that habitats occupied by wild boar at the front of expansion greatly changed, passing from highly forested (representing > 50% of the cover in grids occupied in 1981-1985) to highly agricultural areas (representing >40% of the cover in grids occupied in 2006-2010) (Fig. 5).

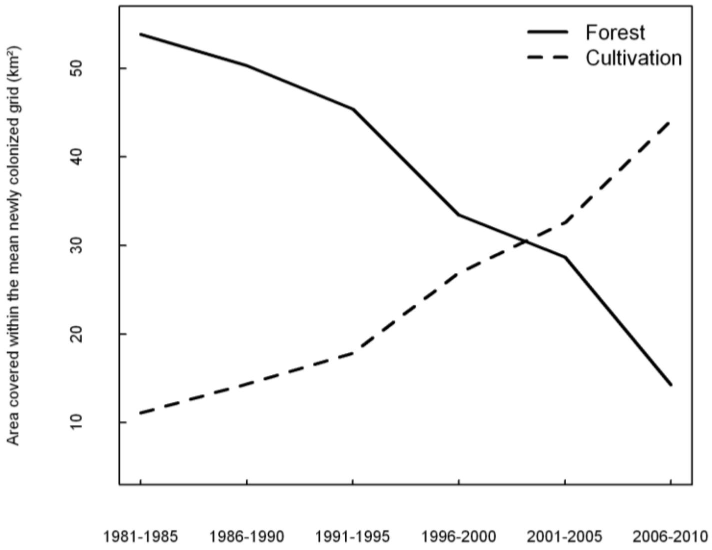

Fig. 5 Forest and cultivation cover characteristics of gird newly occupied by wild boar during the colonization process, Wallonia, Belgium, 1981-2010.

Discussion

We demonstrated that the range expansion was characterized by a linear increase in radial expansion in the first phases followed by an exponential trend starting the 2000's. Our models support the 'lack of population control' (density-dependent) and the landscape (habitat-dependent) hypotheses but do not support the climatic and the human-modified environment hypotheses. Despite the wide occupancy of wild boar within its native range, our research is the first to analyse the dynamics of wild boar colonisation patterns in agro-forested landscapes. Previous studies mainly focused on the expansion or arrival in peri-urban areas

(Cahill and Llimona 2004, Licoppe et al. 2014), corresponding more to range-filling processes rather than increase of range margin or recolonizing process (Carey et al. 2012).

The expansion pattern suggests that the wild boar population almost continuously diffused in the environment. Such a diffusion process occurs when dispersing individuals remains in the neighbourhood of the parent population along the front of expansion, patterns observed in wild boar (Cousse et al. 1994). Over three decades, mean marginal velocity of wild boar expansion in Belgium was similar to estimates of an expanding wild boar population in Sweden (4.8±3.9 km/year; Truvé et al. 2004). Velocity however did not reach values of 50 to 70 km per year observed in the north-eastern range of the species helped by intentional reintroduction (Danilkin 2001, Erkinaro et al. 1982). However, we observed increased velocity in the last periods of colonization, coinciding with the arrival of wild boar population in suboptimal habitats, poor in forest and maize cover, where animal usually respond with higher movement rates (Lubina and Levin 1988).

Proximity to high population density is an important drivers of the colonization process in terrestrial mammal species (Acevedo et al. 2005, Clobert et al. 2012). This factor was already at the basis of the range expansion of wild boar at its north-eastern distribution margin (Danilov and Panchenko 2012). The recognition of the ‘lack of control’ hypothesis suggests that current harvest pressure along the wild boar expansion margin is insufficient to limit wild boar recolonization of former range. We suggest that the lack of efficiency of the hunting activities is a result of both the difficulties to control animal populations in heterogeneous environments (Skogland 1991) and the observed decrease in the number of hunters. The decrease of hunter is consistent with similar trends observed throughout Europe (Massei et al. 2014, Milner et al. 2006) and Northern America (Riley et al. 2003). The decrease in number of hunters likely does not allow to hunt sufficiently the species and to reach to acceptable population size. These observations urge on the need to reconsider hunting in our modern societies and to promote more positively the role played by hunters in the management of wildlife populations. Not only in terms of direct population control and limiting distribution (Saito et al. 2014), but also in its role of creating a landscape of fear influencing largely animal distribution and behaviour (Cromsigt et al. 2013, Tolon et al. 2009). However, role of hunters can be ambiguous, so that behind the 'lack of control' hypothesis might also lies others factors, not directly related to hunting effort, for which we could not account for. Specifically, anthropogenic activities mostly aiming at increasing possibilities of recreational hunting and promoting population size increase such as intentional rewilding (Hearn et al. 2014), supplementary feeding (Milner et al. 2014) or illegal restocking of hybrid captive-reared wild boars (Frantz et al. 2013) can occur and favour the diffusion of the species and explain the role played by density in the colonization process. It is important to notice that the population density variables is also likely influenced by climatic conditions (higher winter survival (Melis et al. 2006) and food availability (Bieber and Ruf 2005).

Forest cover was a significant variable in the latter stages of the colonization process. This suggests wild boar though it entered a more agrarian landscape remains a forest dwelling species, and is consistent with the role played by forest habitat at both large (Danilkin 2001) and fine scale (Gerard et al. 1991). Our result confirm previous finding that mixture of forest and agricultural landscapes best explained the range expansion of wild boar (Saito et al. 2012). In Mediterranean regions, returns or expansions of wild ungulates are related rural depopulation and land abandonment (Acevedo et al. 2011, Hearn et al. 2014), in our study area however, the region is characterized by an increase of the rural demographic pressure (Thomsin 2000).

Contrary to our expectation, changes in the European agricultural policy in the 1980's promoting crops potentially favourable for wild boar (van Vliet et al. 2015) did not influence directly the range expansion. In contrast, agricultural land was negatively correlated to the probability of colonization during the two first colonization periods, and slowed down the expansion process. While cultivation did not drive population spread, this habitat is known to facilitate movement at the local and individual scales (Thurfjell et al. 2009). Seasonal importance of cultivation in bringing energy-rich food and cover for wild boar (Keuling et al. 2009, Morelle and Lejeune 2014), favouring fertility and population growth (Geisser and Reyer 2005, Rosell et al. 2012), is well-documented.

The widespread increase in numbers and geographical distribution together with the ability of wild boar to colonize new areas within its native range questions the current status of the species in many countries, as whether to considerer the wild boar as a game species or more as a pest in some areas of its native range (Mentaberre et al. 2014, Ropars-Collet and le Goffe 2011). The consequences of the observed expansion of wild boar in agro-forested landscapes can be highly detrimental considering the major influence wild boar can have on agricultural ecosystems (Herrero et al. 2006, Schley and Roper 2003).

We suggest that careful management policies, e.g. maintain continuous hunting pressure along the expanding front of expansion, should be undertaken to increase the efficiency and induced role of hunting activities on animal population (Cromsigt et al. 2013). However, management strategies aiming at controlling population should also account for unintended consequences due to the ability of the species to cope with high hunting pressure and by adapting life history strategy (Gamelon et al. 2011).

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References

Acevedo, P. and Cassinello, J. 2009. Human-Induced Range Expansion of Wild Ungulates Causes Niche Overlap between Previously Allopatric Species: Red Deer and Iberian Ibex in Mountainous Regions of Southern Spain. - Annales Zoologici Fennici 46: 39-50.

Acevedo, P. et al. 2005. Environmental constraints in the colonization sequence of roe deer (Capreolus capreolus Linnaeus, 1758) across the Iberian Mountains, Spain. - J. Biogeogr. 32: 1671–1680.

Acevedo, P. et al. 2011. Past, present and future of wild ungulates in relation to changes in land use. - Landscape Ecol. 26: 19-31.

Bieber, C. and Ruf, T. 2005. Population dynamics in wild boar *Sus scrofa*: ecology, elasticity of growth rate and implications for the management of pulsed resource consumers. - J. Appl. Ecol. 42: 1203-1213.

Brook, R. K. and van Beest, F. M. 2014. Feral wild boar distribution and perceptions of risk on the central Canadian prairies. - Wildl. Soc. Bull. 38: 486-494.

Buczkowski, G. 2010. Extreme life history plasticity and the evolution of invasive characteristics in a native ant. - Biol. Invasions 12: 3343-3349.

Burnham, K. P. and Anderson, D. R. 2002. Model Selection and Multi-Model Inference. A Practical Information-Theoretic Approach. - Springer.

Cahill, S. and Llimona, F. 2004. Demographics of a wild boar *Sus scrofa* Linnaeus, 1758 population in a metropolitan park in Barcelona. - Galemys 16 (n° special): 37-52.

Cahill, S. et al. 2012. Characteristics of wild boar (*Sus scrofa*) habituation to urban areas in the Collserola Natural Park (Barcelona) and comparison with other locations. - Anim. Biodivers. Conserv. 35: 221-233.

Carey, M. P. et al. 2012. Native invaders – challenges for science, management, policy, and society. - Frontiers in Ecology and the Environment 10: 373-381.

Chen, I. C. et al. 2011. Rapid range shifts of species associated with high levels of climate warming. - Science 333: 1024-1026.

Clobert, J. et al. 2012. Dispersal Ecology and Evolution. - OUP Oxford.

Commission, E. 2012. Status, management and distribution of large carnivores – bear, lynx, wolf & wolverine – in Europe: Part 1. - In: Kaczensky, P., et al. (eds.). - European Commission, p. 72.

Cousse, S. et al. 1994. Use of space by juveniles in relation to their postnatal range, mother, and siblings: an example in the wild boar, *Sus scrofa* L. - Canadian Journal of Zoology 72: 1691-1694.

Cromsigt, J. P. G. M. et al. 2013. Hunting for fear: innovating management of human–wildlife conflicts. - J. Appl. Ecol. 50: 544-549.

Danilkin, A. A. 2001. The wild boar: an unprecedented spread or restoration of the species range? - Doklady Biological Sciences 380: 457–460.

Danilov, P. I. and Panchenko, D. V. 2012. Expansion and some ecological features of the wild boar beyond the northern boundary of its historical range in European Russia. - Russian J. Ecol. 43: 45-51.

Dormann, C. F. et al. 2012. Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. - Ecography.

Erkinaro, E. et al. 1982. Occurence and spread of the wild boar (*Sus scrofa*) in eastern Fennoscandia. - Memoranda Societatis pro Fauna et Flora Fennica 58: 39-47.

Frantz, A. C. et al. 2012. Comparative landscape genetic analyses show a Belgian motorway to be a gene flow barrier for red deer (*Cervus elaphus*), but not wild boars (*Sus scrofa*). - Mol. Ecol. 21: 3445-3457.

Frantz, A. C. et al. 2013. Genetic evidence for introgression between domestic pigs and wild boars (Sus scrofa) in Belgium and Luxembourg: a comparative approach with multiple marker systems. - Biol. J. Linn. Soc. 110: 104-115.

Gamelon, M. et al. 2011. High hunting pressure selects for earlier birth date: wild boar as a case study. - Evolution 65: 3100-3112.

Geisser, H. and Reyer, H.-U. 2005. The influence of food and temperature on population density of wild boar *Sus scrofa* in the Thurgau (Switzerland). - J. Zool. 267: 89-96.

Gerard, J.-F. et al. 1991. Habitat use of wild boar in a French agroecosystem from late winter to early summer. - Acta Theriol 36: 119-129.

Gortázar, C. et al. 2006. Disease risks and overabundance of game species. - Eur. J. Wildl. Res. 52: 81-87.

Gurevitch, J. and Padilla, D. K. 2004. Are invasive species a major cause of extinctions? - Trends in Ecology & Evolution 19: 470-474.

Hearn, R. et al. 2014. The cultural and land use implications of the reappearance of the wild boar in North West Italy: A case study of the Val di Vara. - Journal of Rural Studies 36: 52-63.

Heather, C. and Dukes, J. S. 2007. Impacts of Invasive Species on Ecosystem Services. - In: Nentwig, W. (ed.) Biol. Invasions. Springer Berlin Heidelberg, pp. 217-237.

Herrero, J. et al. 2006. Diet of wild boar *Sus scrofa* L. and crop damage in an intensive agroecosystem. - European Journal of Wildlife Research 52: 245–250.

Ipcc. 2014. Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Field, C.B., V.R. Barros, D.J. Dokken, K.J. Mach, M.D. Mastrandrea, T.E. Bilir, M. Chatterjee, K.L. Ebi, Y.O. Estrada, R.C. Genova, B. Girma, E.S. Kissel, A.N. Levy, S. MacCracken, P.R. Mastrandrea, and L.L. White (eds.)]. - Cambridge University Press.

Jeschke, J. M. and Strayer, D. L. 2005. Invasion success of vertebrates in Europe and North America. - Proc. Natl. Acad. Sci. U. S. A. 102: 7198-7202.

Jeschke, J. M. and Strayer, D. L. 2006. Determinants of vertebrate invasion success in Europe and North America. - Global Change Biology 12: 1608-1619.

Kaplan, J. O. et al. 2009. The prehistoric and preindustrial deforestation of Europe. - Quaternary Science Reviews 28: 3016-3034.

Keuling, O. et al. 2013. Mortality rates of wild boar *Sus scrofa* L. in central Europe. - Eur J Wildl Res online first: 1-10.

Keuling, O. et al. 2010. Hunter feedback of individually marked wild boar Sus scrofa L.: Dispersal and efficiency of hunting in northeastern Germany. - European Journal of Wildlife Research 56: 159-167.

Keuling, O. et al. 2009. Commuting, shifting or remaining?. Different spatial utilisation patterns of wild boar *Sus scrofa* L. in forest and field crops during summer. - Mammalian Biology 74: 145-152.

Lensink, R. 1997. Range expansion of raptors in Britain and the Netherlands since the 1960s: testing an individual-based diffusion model. - J. Anim. Ecol. 66.

Licoppe, A. et al. 2014. Enquête international sur le sanglier en zone péri-urbaine [International survey on peri-urban wild boar populations]. - For. Wall. 131: 3-16.

Long, J. L. 2003. Introduced mammals of the world. Their history, distribution and influence. - CSIRO Publishing.

Lowe, S. et al. 2004. 100 of the world’s worst invasive alien species: a selection from the global invasive species database. - In: (IUCN), T. I. S. S. G. I. a. s. g. o. t. S. S. C. S. o. t. W. C. U. (ed.), p. 12.

Lubina, J. A. and Levin, S. A. 1988. The spread of a reinvading species: range expansion in the California sea otter. - The American Naturalist 131: 526-543.

Massei, G. and Genov, P. 2004. The environmental impact of wild boar. - Galemys 16: 135–145.

Massei, G. et al. 2014. Wild boar populations up, numbers of hunters down? A review of trends and implications for Europe. - Pest Manage. Sci.: n/a-n/a.

Melis, C. et al. 2006. Biogeographical variation in the population density of wild boar (*Sus scrofa*) in western Eurasia. - J. Biogeogr. 33: 803-811.

Mentaberre, G. et al. 2014. Long-Term Assessment of Wild Boar Harvesting and Cattle Removal for Bovine Tuberculosis Control in Free Ranging Populations. - PLoS ONE 9: e88824.

Milner, J. M. et al. 2006. Temporal and spatial development of red deer harvesting in Europe: biological and cultural factors. - Journal of Applied Ecology 43: 721-734.

Milner, J. M. et al. 2014. To feed or not to feed? Evidence of the intended and unintended effects of feeding wild ungulates. - The Journal of Wildlife Management 78: 1322-1334.

Morelle, K. and Lejeune, P. 2014. Seasonal variations of wild boar Sus scrofa distribution in agricultural landscapes: a species distribution modelling approach. - European Journal of Wildlife Research: 1-12.

Olson, L. J. 2006. The economics of terrestrial invasive species: a review of the literature. - Agricultural and Resource Economics Review 35: 178.

Park, C.-R. and Lee, W.-S. 2003. Development of a GIS-based habitat suitability model for wild boar *Sus scrofa* in the Mt. Baekwoonsan region, Korea. - Mammal Study 28: 17-21.

Perrings, C. et al. 2010. International cooperation in the solution to trade-related invasive species risks. - Ann. N. Y. Acad. Sci.

Podgórski, T. et al. 2013. Spatiotemporal behavioral plasticity of wild boar (*Sus scrofa*) under contrasting conditions of human pressure: primeval forest and metropolitan area. - J. Mammal. 94: 109-119.

Preuss, S. et al. 2014. Evaluating range-expansion models for calculating nonnative species' expansion rate. - Ecology and Evolution 4: 2812-2822.

Prevot, C. and Licoppe, A. 2013. Comparing red deer (Cervus elaphus L.) and wild boar (Sus scrofa L.) dispersal patterns in southern Belgium. - Eur. J. Wildl. Res.: 1-9.

Putman, R. et al. (eds.). 2011. Ungulate management in Europe: Problems and practice.

R Core Team. 2013. R: A language and environment for statistical computing. - R Foundation for Statistical Computing.

Riley, S. J. et al. 2003. Deer populations up, hunter populations down: Implications of interdependence of deer and hunter population dynamics on management. - Ecoscience 10: 455-461.

Ropars-Collet, C. and le Goffe, P. 2011. Pest or game? An economic analysis of big animals hunting in France. - Revue d'Etudes en Agriculture et Environnement 92: 161-181.

Rosell, C. et al. 2012. Reproduction of wild boar in a cropland and coastal wetland area: implications for management. - Anim. Biodivers. Conserv. 35: 209-217.

Rosvold, J. and Andersen, R. 2008. Wild Boar in Norway – is Climate a Limiting Factor? Zoologisk rapport. - Norges Teknisk-naturvitenskapelige Universitet, p. 24.

Saez-Royuela, C. and Telleria, J. L. 1986. The increased population of the wild boar (*Sus scrofa L.*) in Europe. - Mamm. Rev. 16: 97-101.

Saito, M. et al. 2012. Forecasting the range expansion of a recolonising wild boar Sus scrofa population. - Wildl. Biol. 18: 383-392.

Saito, M. U. et al. 2014. Range-expanding wildlife: modelling the distribution of large mammals in Japan, with management implications. - International Journal of Geographical Information Science: 1-16.

Schley, L. and Roper, T. J. 2003. Diet of wild boar *Sus scrofa* in Western Europe, with particular reference to consumption of agricultural crops. - Mamm. Rev. 33: 43-56.

Seebens, H. et al. 2013. The risk of marine bioinvasion caused by global shipping. - Ecology Letters 16: 782-790.

Servanty, S. et al. 2009. Pulsed resources and climate-induced variation in the reproductive traits of wild boar under high hunting pressure. - J. Anim. Ecol. 78: 1278-1290.

Shigesada, N. and Kawasaki, K. 1997. Biological invasions: theory and practice. - Oxford University Press.

Silva, T. et al. 2002. A model for range expansion of an introduced species: the common waxbill *Estrilda astrild* in Portugal. - Divers. Distrib. 8: 319-326.

Simberloff, D. and Rejmanek, M. 2010. Encyclopedia of Biological Invasions. - University of California Press.

Skellam, J. G. 1951. Random dispersal in theoretical populations. - Biometrika 38: 196-218.

Skogland, T. 1991. What are the effects of predators on large ungulate populations? - Oikos 61: 401-411.

SPW. 2012. Les indicateurs clés de l'environnement wallon 2012. - In: Editions, S. (ed.), p. 160.

Thomas, C. D. et al. 2001. Ecological and evolutionary processes at expanding range margins. - Nature 411: 577-581.

Thomsin, L. 2000. La reprise démographique rurale en Wallonie et en Europe du Nord-Ouest. - Espace, populations, sociétés: 83-99.

Thurfjell, H. et al. 2009. Habitat use and spatial patterns of wild boar *Sus scrofa* (L.): agricultural fields and edges. - European Journal of Wildlife Research 55: 517-523.

Tolon, V. et al. 2009. Responding to spatial and temporal variations in predation risk: space use of a game species in a changing landscape of fear. - Canadian Journal of Zoology 87: 1129-1137.

Toussaint, M. et al. 2011. Les Néandertaliens du bassin mosan belge : bilan 2006-2011. - Bulletin des Chercheurs de la Wallonie hors-série no 4: 149-196.

Truvé, J. et al. 2004. Dispersal in relation to population density in wild boar (*Sus scrofa*). - Galemys 16 (n° special): 75-82.

Valéry, L. et al. 2013. Another call for the end of invasion biology. - Oikos 122: 1143-1146.

Valéry, L. et al. 2008. In search of a real definition of the biological invasion phenomenon itself. - Biol. Invasions 10: 1345-1351.

Valéry, L. et al. 2009. Ecosystem-level consequences of invasions by native species as a way to investigate relationships between evenness and ecosystem function. - Biol. Invasions 11: 609-617.

Valéry, L. et al. 2009. Invasive species can also be native…. - Trends Ecol. Evol. 24: 585.

van Vliet, J. et al. 2015. Manifestations and underlying drivers of agricultural land use change in Europe. - Landsc. Urban Plann. 133: 24-36.

Veeroja, R. and Männil, P. 2014. Population development and reproduction of wild boar (*Sus scrofa*) in Estonia. - Wildlife Biology in Practice 10: 17-21.

With, K. A. 2002. The landscape ecology of invasive spread. - Conserv. Biol. 16: 1192-1203.

Supplementary material - Appendix 1

Table A1. A priori models exploring the effect of xyz variable wild boar expansion, Wallonia, Belgium, 1981-2010. AICc = Akaike Information Criteria adjusted for small sample sizes; ΔAICc = (AICc) – $(\text{AICc})_{\text{min}}$; w = Akaike weight. Only candidate models with ΔAICc < 2 selected as final models are shown.

Period 1981-1985					
Model no.	Model set	K	AICc	varAICc	Wt
11	Landscape, control, agriculture	7	50.62	0.00	0.37
5	Landscape, control	5	51.65	1.02	0.22
14	control, agriculture, climate	5	52.64	2.01	0.14

Parameter	Estimate	SE	CI lower	CI upper
Forest	0.073	0.0540	-0.0034	0.1793
Rivers	0.00002	1.641	-0.00002	0.00005
Agricover	-0.164	0.1624	-0.5164	-0.00940
Grasslands	-0.145	0.04546	-0.1339	0.0874
Roads	0.0000004	0.000006	-0.00001	0.00001
ndens	0.122	0.04863	0.0260	0.2188

Period 1986 - 1990					
Model no.	Model set	K	AICc	varAICc	Wt
5	Landscape, control	5	63.11	0.00	0.27
14	control, agriculture, climate	5	63.30	0.20	0.24
7	Landscape, climate	4	64.26	1.15	0.15

Parameter	Estimate	SE	CI lower	CI upper
Forest	0.0567	0.0447	-0.0235	0.1394
Rivers	0.000008	0.00001	-0.00002	0.00004
Roads	0.000001	0.000003	-0.000005	0.000009
ndens	0.0586	0.0396	0.01073	0.1335
Agricover	-0.0555	0.0903	-0.3018	-0.0643
Grasslands	-0.0220	0.0398	-0.1509	0.0060
tmean	-1.272	1.313	-4.2294	0.4057

Period 1991 - 1995

Model no.	Model set	K	AICc	varAICc	Wt
5	Landscape, control	5	65.80	0.00	0.60
12	Landscape, control, climate	6	67.72	1.92	0.23
11	Landscape, control, agriculture	7	69.80	4.00	0.08

Parameter	Estimate	SE	CI lower	CI upper
Forest	0.0950	0.0327	0.03010	0.1599
Rivers	0.000004	0.00001	-0.00002	0.00003
Roads	0.000007	0.000003	-0.000005	0.000006
ndens	0.0697	0.0276	0.0149	0.1245
tmean	0.1879	0.6713	-1.5820	2.9409

Period 1996 - 2000

Model no.	Model set	K	AICc	varAICc	Wt
5	Landscape, control	5	42.50	0.00	0.52
12	Landscape, control, climate	6	44.43	1.94	0.20
11	Landscape, control, agriculture	7	44.69	2.19	0.18

Parameter	Estimate	SE	CI lower	CI upper
Forest	0.1958	0.0690	0.05802	0.3337
Rivers	-0.0000005	0.00002	-0.00003	0.00003
Roads	0.000004	0.000003	-0.000002	0.000009
ndens	0.0883	0.0374	0.0136	0.1630
tmean	-0.3454	1.1290	-4.9873	2.4761

Period 2001- 2005

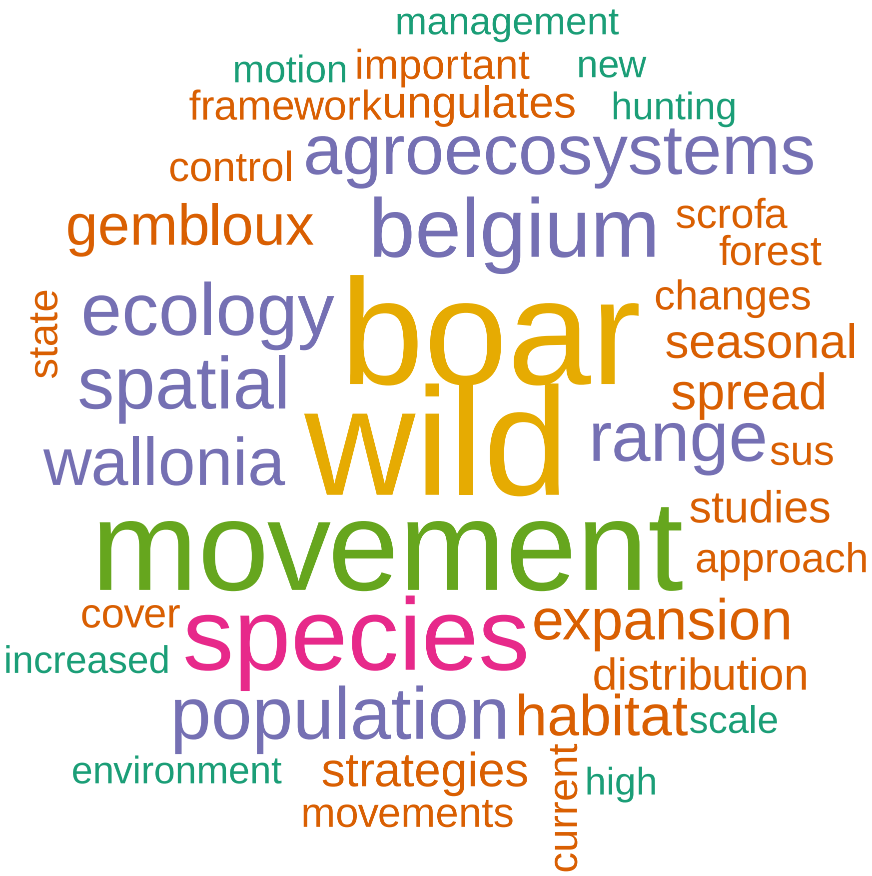
Model no.	Model set	K	AICc	varAICc	Wt
5	Landscape, control	5	25.00	0.0	0.72
12	Landscape, control, climate	6	26.45	1.45	0.21
11	Landscape, control, agriculture	7	26.70	1.70	0.06

Parameter	Estimate	SE	CI lower	CI upper
Forest	0.2146	0.0718	0.06204	0.3422
Rivers	-0.0000005	0.00002	-0.00003	0.00003
Roads	0.000004	0.000003	-0.000002	0.000008
ndens	0.0772	0.0396	0.0128	0.1717
tmean	-0.3364	1.1118	-5.2836	3.01862

Period 2006- 2010

Model no.	Model set	K	AICc	varAICc	Wt
8	Agriculture, control	4	54.55	0.00	0.18
5	Landscape, control	5	55.32	0.77	0.13
10	Agriculture, climate	4	55.53	0.98	0.11

Parameter	Estimate	SE	CI lower	CI upper
Forest	0.0239	0.0480	-0.0310	0.1950
Rivers	0.000007	0.00001	-0.000003	0.00005
Roads	0.00000007	0.0000011	-0.000005	0.000006
ndens	0.0371	0.0418	-0.0159	0.1365
Agricover	-0.0105	0.0339	-0.1027	0.0678
Grasslands	0.0724	0.0830	-0.0325	0.2725
tmean	-1.0550	1.8690	-7.0332	1.3410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