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

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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).

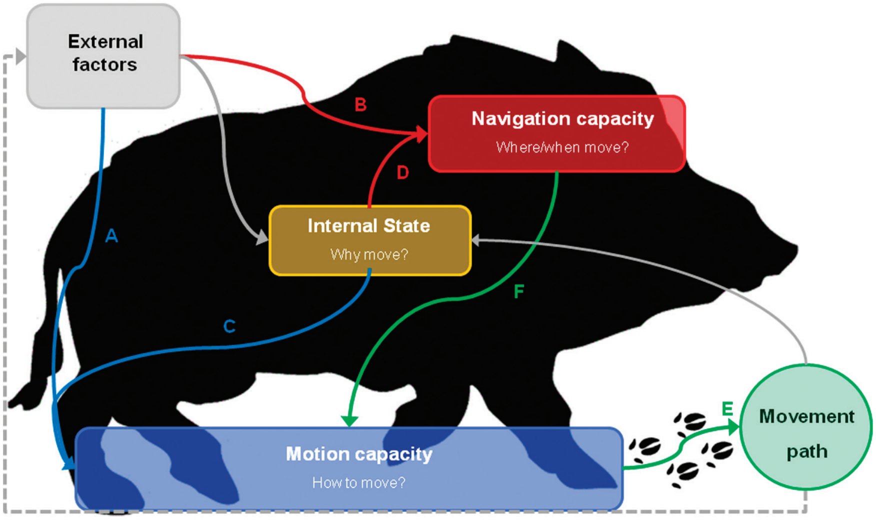

Figure 1. Illustration of the conceptual framework for movement ecology, adapted from Nathan et al. (2008). The framework is composed of four main components: internal state (physiological state affecting motivation to move), motion capacity (biomechanical or morphological properties of the individual 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

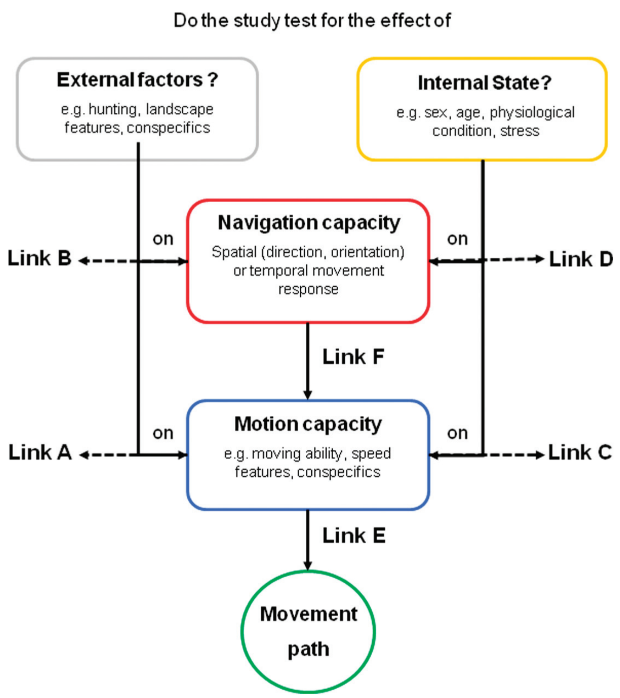

Figure 2. Schematic description of the method used to assess components and links of the movement ecology framework considered by the movement focal studies.

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%).

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,

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

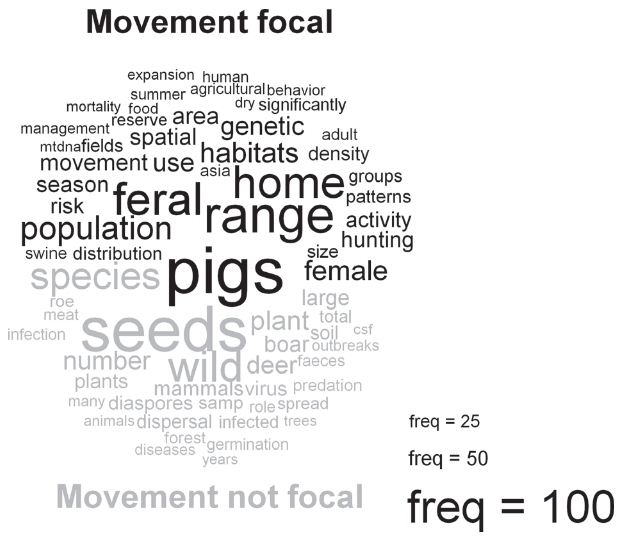

Figure 3. Word cloud representing the 70 most frequent words in the abstract of the 'hit' papers. In the upper part (black) are words related to the movement focal studies, and in the lower part (grey) are words related to wild boar but where movement was not focal to the study. As indicated by the frequency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

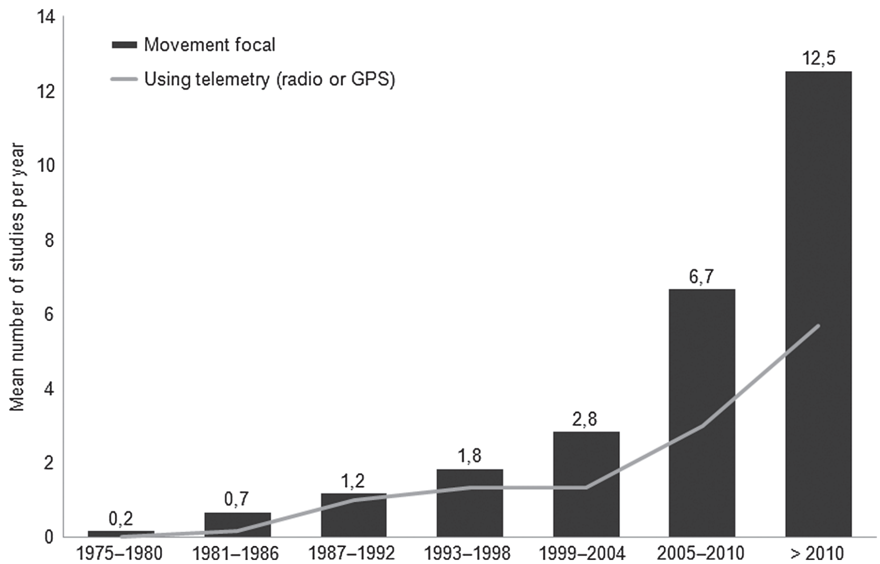

Figure 4. Temporal evolution of the number of movement focal studies (black bar) and those based on telemetry tracking methods (grey line).

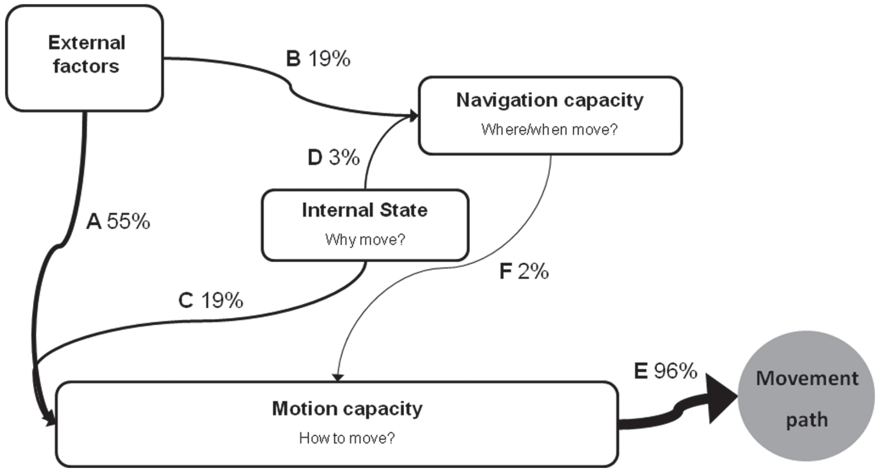

Figure 5. Percentage of studies per link between components of the movement ecology framework. An example of link A is a study on the effect of season on the movement pattern (feeding and exploring) and rate (mean distance walked) of wild pigs. An example of link B is a study on the effect of geographic 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

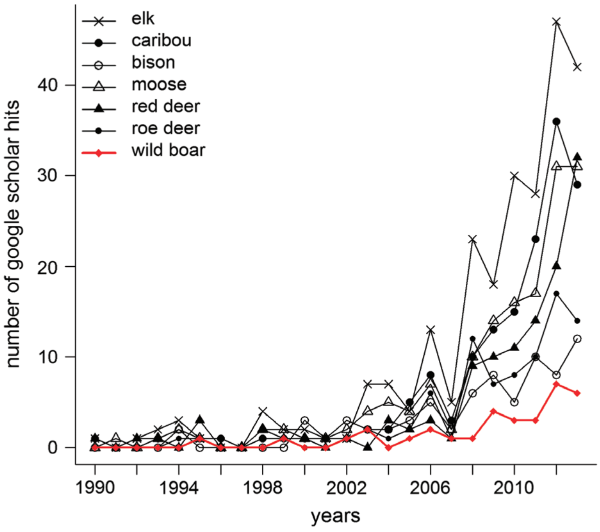

Figure 6. Evolution of the number of hits resulting from a Google scholar search about different ungulates species and movement ecology. For every of these species, we used the following search terms: "common name of the species" AND "movement ecology".

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 socio-spatial 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.