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Effect of relatedness on spatial and social structure  
of the wild boar *Sus scrofa* population  
in Białowieża Primeval Forest

Doctoral dissertation

Thesis conducted at the Mammal Research Institute,  
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Wpływ spokrewnienia na strukturę przestrzenną  
i socjalną populacji dzika *Sus scrofa*  
w Puszczy Białowieskiej

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Maj 2013

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## **ABSTRACT**

Fitness benefits of sociality increase individual survival and reproductive success through a complex network of social interactions. Kin selection theory predicts that individuals increase their inclusive fitness through altruistic behaviours directed towards kin. Thus, preferential social interactions with relatives lead to the emergence of kin structures in the social system. Cohesive social groups, female philopatry, and high reproductive output of wild boar creates conditions for cooperation through kin selection and make the species a good biological model for studying kin structures. Yet, the role of kinship in shaping the social structure of wild boar populations is still poorly understood.

The main goal of this study, conducted in Białowieża Primeval Forest (BPF) in 2007-2011, was to explore spatial and temporal patterns of social interactions in the wild boar population, and to determine the role of relatedness in shaping the emergent social structure of the species.

A combination of behavioural (telemetry) and genetic (microsatellite DNA) data were used to investigate group structure and composition, dispersal patterns, and population structure of wild boar. Network techniques, association analyses, and estimates of lagged association rates were used to determine temporal and spatial structure of the social interactions in the studied population. A total of 141 wild boar were captured, 114 of which belonged to 16 marked groups and the rest were either solitary or belonged to unmarked groups. Telemetry-marked animals ( $n = 75$ ) included all solitary wild boar and, on average, 66% of the groups' members. Genetic analyses included all captured animals and samples collected by hunters in the Polish and Belarusian parts of the BPF ( $n = 411$ ). All individuals were genotyped with a panel of 16 microsatellite loci.

The average family group size estimated from the trapping data was 7 individuals. This result was consistent with analyses based on social interactions alone (association rates and network analysis). The vast majority of adult females and young animals were associated in groups, whereas adult males were mostly solitary. Individuals associated in groups were significantly more genetically related to each other than non-associating, solitary individuals. On average, the intra-group level of relatedness corresponded to second-degree relatives. Relatedness within a group was negatively correlated with group size. Members of the family groups showed extensive spatial overlap, whereas animals from different family groups shared little space.

Wild boar in the study population formed non-random, preferential associations which were largely stable and long-lasting. The temporal stability of associations was particularly strong among adult females and animals forming family groups. Conversely, adult males

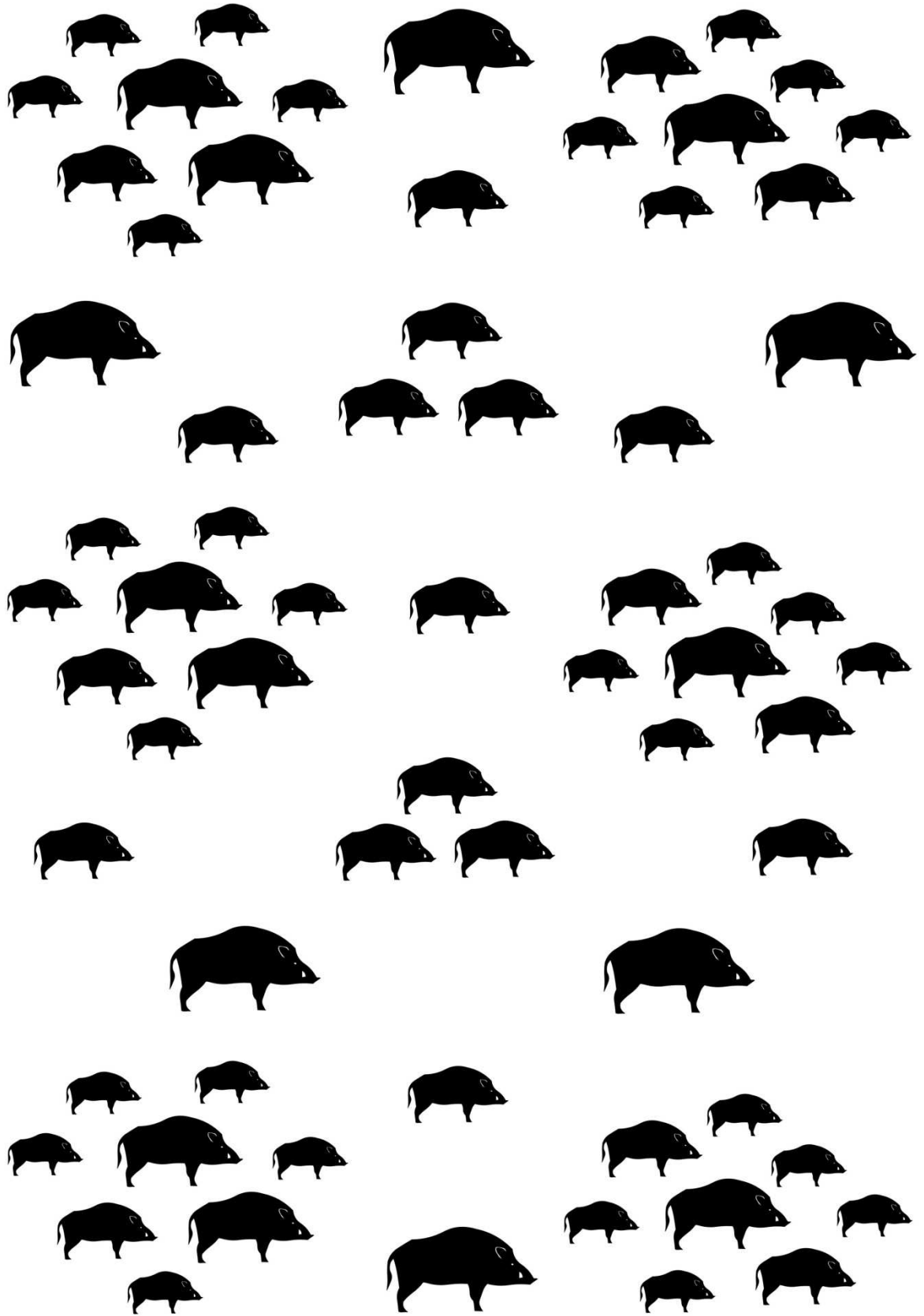
formed short-lived associations disintegrating within a few days. High temporal stability of associations observed among animals forming groups implies strong group cohesion. There was a positive correlation between strength of social bond and genetic relatedness but kin-targeted interactions extending beyond spatial proximity of individuals were observed only among females.

On the population level, there was a negative relationship between geographic distance and genetic relatedness. Spatial genetic structure was detected at small spatial scale corresponding to few home ranges. Genetic structure was maintained at the same distance in males and females. However, females showed a stronger relationship between genetic and spatial distance at short distances (0-1 km), whereas males showed stronger structuring in the distance class of 1-5 km. Assignment index provided little evidence for sex-biased dispersal, yet indicated a tendency towards greater dispersal in males. Telemetry data on dispersal provided results consistent with genetic data. Sex bias was manifested in dispersal distance, but not dispersal frequency, with females usually settling in the direct vicinity of the maternal home range and males few home ranges away from the natal site. Dispersal occurred at the age of 18-21 months.

The social network, derived solely from association data, was spatially structured with well defined and cohesive social units. The units were also genetically distinct, with high intra-group and low inter-group genetic relatedness. Space utilised by the members of a given social unit overlapped extensively while little overlap was observed across social units. The genetic structure in the network can be interpreted as an emergent property of philopatry and spatial segregation of social groups. However, spatial distribution and overlap of individuals could not fully explain the association patterns and network structure. Association and genetic data indicated that active social preferences and targeted interactions played important roles in shaping the social structure of the population. The close match of the social structure revealed in social units and family groups (obtained from trapping data) indicated that they mirror the same level of social organisation.

Sociality of wild boar, estimated by three network centrality measures, generally decreased with age of the individuals, and magnitude of age effect was modified by sex. Young wild boars showed the strongest grouping tendency and were the most diversely connected within the networks. The onset of dispersal marked a decrease in sociality, which was manifested stronger in males than in females. These results highlight the role of young wild boar in maintaining cohesion of the social network. Changes in sociality mirrored major transitions in wild boar ontogeny.





## 1. INTRODUCTION

The variety of mammalian social systems arises from the attempts individuals make to maximise their fitness, both in direct and indirect way. Direct fitness benefits of sociality increase individual survival and reproductive success through a complex network of social interactions. Those cooperative interactions, maintained by mutualism and behavioural reciprocity, can provide individuals with assets vital for survival (access to food, shelter, help in predator avoidance) and reproduction (breeding sites, mating partners) (Trivers 1971, Clutton-Brock 2009). Kinship is not a prerequisite for these type of interactions to occur. On the contrary, indirect fitness benefits that animals obtain from living socially, originate from kin selection and involve relatedness between interacting parties. The cost an individual is willing to pay for exhibiting beneficial behaviour is proportional to the relatedness of the recipient to the donor (Hamilton 1964). Individuals increase their inclusive fitness through altruistic behaviours directed towards kin. Naturally, cumulative benefits which an individual experiences from sociality are often a result of combined direct and indirect effects that can be temporally delayed what makes telling the two components apart challenging.

The structural properties of the social system (group size and dynamics, ranging patterns, duration and stability of sex- and age-specific social bonds) emerge from interactions between internal (species) and external (environment) factors (Crook et al. 1976). Internal drivers involve species characteristics (such as mobility, dietary demands, susceptibility to predation) and factors intrinsic to individuals (such as preferred associates, social role) (Crook et al. 1976, Gerard and Richard-Hansen 1992, Lusseau and Newman 2004). Environmental drivers comprise density-dependent factors such as food availability and predation (Skogland 1991, L'Heureux et al. 1995, Baird and Dill 1996, Kie et al. 1999) and density-independent variables such as climatic conditions and habitat structure (Pays et al. 2007). Environmental factors, mainly food distribution and predation risk, are the major determinants of mammalian social organisation and structure (Rubenstein and Wrangham 1986, Lott 1991). Environmental factors are coupled with different potential reproduction rates of males and females in shaping mammalian social and mating systems. Females lifetime reproductive success is primarily constrained by food resources, whereas that of males is mainly limited by access to mates (Emlen and Oring 1977, Clutton-Brock and Harvey 1978). Therefore, food abundance and distribution largely determine the distribution of females, while males are expected to be distributed according to the number and distribution of females, as well as presence and behaviour of the other males (Emlen and Oring 1977).

Next to environmental and behavioural components, demographic processes play an important role in shaping social systems (Lott 1991, Pope 1998), with dispersal being one of

the key factors (Chepko-Sade and Tang Halpin 1987, Perrin et al. 2012). Inclusive fitness can be increased through altruistic behaviours directed towards kin thus promoting philopatry. However, increased local relatedness and emerging kin structures can lead to negative consequences of inbreeding and kin competition if all the offspring were to stay in the natal area (Hamilton and May 1977, Gandon and Michalakis 2001, Keller and Waller 2002). Natal dispersal, which is the movement of an individual from its birth site to the site of its first reproduction (Howard 1960), has evolved as a strategy to circumvent negative effects of mating and competing with relatives (Gandon and Michalakis 2001). In mammals, females tend to remain in their natal area or group, whereas males disperse (Greenwood 1980, Dobson 1982). This pattern is expected to be more pronounced in social species owing to the inclusive benefits of philopatry, such as familiarity with food resources and helping behaviours, which are vital for female reproductive success (Clutton-Brock and Lukas 2012, Dobson et al. 2012). The social structure emerging from the interplay of behavioural, environmental, and demographic factors greatly influences transfer of genes (Sugg et al. 1996, Storz 1999), diseases (Loehle 1995, Read and Keeling 2003), and information (McComb et al. 2001, Danchin et al. 2004). Genetic relationships between individuals can in turn affect their cooperative behaviour (Dobson et al. 1998). Thus, studying genetic structure of the population can enable meaningful inferences on its social organisation (Sugg et al. 1996).

Social structure emerges from non-random distribution, grouping, and ranging patterns of individuals in a population (Crook et al. 1976). Understanding the social structure requires describing patterns of relationships between animals independently of the particular individuals involved (Hinde 1976). Specifically, identifying occurrence, distribution, and composition of social groups helps to reveal individual association preferences and is essential to determine social structure of a population (Whitehead 1997). However, social structuring represents a complex network of interactions between individuals changing in space and time and as such is difficult to quantify. Yet another difficulty arises when meaningful interactions are problematic to describe or observe (e.g. due to habitat structure or species behaviour). Dyadic (between two animals) interactions are the basic elements upon which social structure is built (Hinde 1976). They can be approximated by recording situations in which interactions might potentially occur such as dyadic spatial proximity (association) (Whitehead 1997). Hence, measuring the time two animals spend together using association indices offers a convenient, yet qualitatively simplified, substitute of recording actual interactions (Whitehead and Dufault 1999). Numerous studies have shown that if animals spend more time together than expected by chance, they tend to be socially associated (e.g. Kaminski et al. 2005, Lusseau et al. 2006, Wolf et al. 2007). Analysing the rate at which

associations between individuals changes over time can help characterise the temporal aspect of social structure dynamics (Whitehead 1995, Wiszniewski et al. 2010).

Describing structural properties of a social system requires accounting for spatial and temporal dynamics of the association patterns. This might be particularly challenging in fission-fusion societies, where associations break and reform in response to dynamic effect of ecological factors such as food availability and predation pressure (Wrangham 1982, Henzi et al. 2009). Additionally, associations of the individuals can be structured hierarchically in several levels of organisation from individual to population (e.g. African elephants *Loxodonta africana*, Wittemyer et al. 2005; Galapagos sea lion *Zalophus wollebaeki*, Wolf et al. 2007). Application of an analytical approach based on network theory to animal societies (e.g. Croft et al. 2006, Lusseau et al. 2006, Wolf et al. 2007) offers a powerful tool to explore such complex dynamic systems (Krause et al. 2007). Social network analysis (SNA), originating from physical sciences and later used to study human social systems, help describe individual connectivity, associations and grouping patterns and is therefore well suited to study social structures (Wey et al. 2008).

In recent years, noticeable advances in the study of social systems have been made thanks to application of the SNA. Understanding of how ecological factors (Henzi et al. 2009), social and genetic relationships between individuals (Wolf and Trillmich 2008, Wiszniewski et al. 2010), and individual “personalities” (Lusseau and Newman 2004) shape association patterns and social structure has been greatly improved. Next to describing network architecture, the SNA can quantify an individual’s sociality, i.e. position and connectivity in the network, using centrality measures. Animals with high centrality are either associated with many others or connected with individuals from different social groups. Therefore, those individuals can have disproportionately high effect on social cohesion (Williams and Lusseau 2006), information transfer (Danchin et al. 2004), and group-decision making (Lusseau 2007). Despite its advantages, the network approach has never been applied to study wild boar *Sus scrofa* sociality, which still remains poorly understood. This study utilises the network approach to find subdivision of the population into social units based on social contacts (association) data only. Next, the role of sex and age in maintaining cohesion of the wild boar network is examined, both in terms of temporal stability and structural connectivity.

Matrilineality (females associated by pedigree through female ancestors) is a widespread type of social organisation among suids. It was found for example in babirusa *Babirusa babirusa* (Patry et al. 1995, Clayton and MacDonald 1999), warthog *Phacochoerus africanus* (White et al. 2010), and desert warthog *Phacochoerus aethiopicus*

(Somers 1995). In wild boar, social structure is centred around family groups of adult female(s) with offspring (Hirotani and Nakatani 1987, Dardaillon 1988, Spitz 1992, Nakatani and Ono 1995). Commonly, few families merge to form matrilineal and multigenerational social units (Gabor et al. 1999, Kaminski et al. 2005, Poteaux et al. 2009). Occasionally, the units merge, split or exchange individuals (Gabor et al. 1999, Poteaux et al. 2009), yet patterns and mechanisms of fission-fusion dynamics have not been recognised. Ranges of adult females/family groups overlap extensively (Boitani et al. 1994, Gabor et al. 1999). Solitary adult males temporarily join female groups during the rut (Dardaillon 1988). Mating system is moderately polygynous with adult males assumed to be engaged in roving dominance hierarchy (Hampton et al. 2004, Poteaux et al. 2009). Selective hunting pressure may strongly modify wild boar mating system (level of polygyny) (Poteaux et al. 2009) and social structure (group composition and association patterns) (Iacolina et al. 2009).

The onset of natal dispersal is believed to be associated with reaching sexual maturity by juveniles and starts around one year of age (Truvé and Lemel 2003). Dispersal is generally male-biased and males tend to disperse longer distances compared to females (Truvé and Lemel 2003, Poteaux et al. 2009, Keuling et al. 2010). The majority of dispersal occurs at short distances equalling 1-3 diameters of an average home range (Keuling et al. 2010), although longer dispersals (>10 km) are also observed frequently (Andrzejewski and Jezierski 1978, Truvé and Lemel 2003, Keuling et al. 2010). So far, data on dispersal have been collected using hunters reports on shot individuals which allow only for general conclusions. The complementary approach, which combines fine-scale telemetry data and population-level genetic information, would definitely broaden our understanding of wild boar dispersal patterns in social context. This was one of the goals of my study.

The process of building kin structures through retention of offspring within parental neighbourhood (i.e. philopatry) is stimulated by the inclusive fitness benefits an individual gains (Gaston 1978, Perrin and Lehmann 2001). The higher the local relatedness, the higher the profits from group effects (predator defence, food acquisition) and cooperative behaviours (breeding, sharing knowledge on resources). Consequently, the emerging socio-genetic structure should be characterised by an inverse relationship between genetic and spatial distance and higher intra-group than inter-group relatedness. Indeed, the occurrence of such structures is well documented across a variety of mammalian species, e.g. raccoon *Procyon lotor* (Ratnayeke et al. 2002), polar bear *Ursus maritimus* (Zeyl et al. 2009), sperm whale *Physeter macrocephalus* (Gero et al. 2008), gray mouse lemur *Microcebus murinus* (Wimmer et al. 2002), woodchuck *Marmota monax* (Maher 2009), and Florida black bears *Ursus americanus floridanus* (Moyer et al. 2006). On the other hand, complex social systems are not

always kin-based and they may be maintained by behavioural reciprocity and mutualism (Clutton-Brock 2009, Garroway et al. 2013) or result from the negative demographic effects of hunting (Comer et al. 2005, Iacolina et al. 2009).

Cohesive social groups, female philopatry, and high reproductive output of wild boar creates conditions for cooperation through kin selection and make the species a good biological model for studying kin structures. Yet, the role of kinship in shaping the socio-genetic structure of wild boar populations is poorly understood and only recently has received some attention (Iacolina et al. 2009, central Italy; Poteaux et al. 2009, north-eastern France). Both studies described low levels of intra-group relatedness, especially among adults. Additionally, Iacolina et al. (2009) found no correlation between genetic and spatial distance among adults and associations of unrelated females were frequently observed. Apparent weak kin-structure in this study was attributed to high human-caused mortality altering social structure and wolf *Canis lupus* predation pressure stimulating unrelated individuals (human hunting survivors) to associate. On the other hand, Poteaux et al. (2009) showed that females in spatial proximity were more related to each other than at random, thus providing evidence for kin-based, matrilineal structure. The analysis, however, did not account for the complexity of social interactions, which may act independently of spatial proximity between individuals in shaping association patterns at small spatial scales. Both studies were conducted in heavily hunted populations with potentially strongly modified social structure. The wild boar population in the Białowieża National Park, where this study was conducted, inhabits undisturbed forest habitat and is free of hunting and thus it offers an insight into social relationships unaltered by anthropogenic factors, a situation which is rarely found in Europe.

## 2. AIMS OF THE STUDY

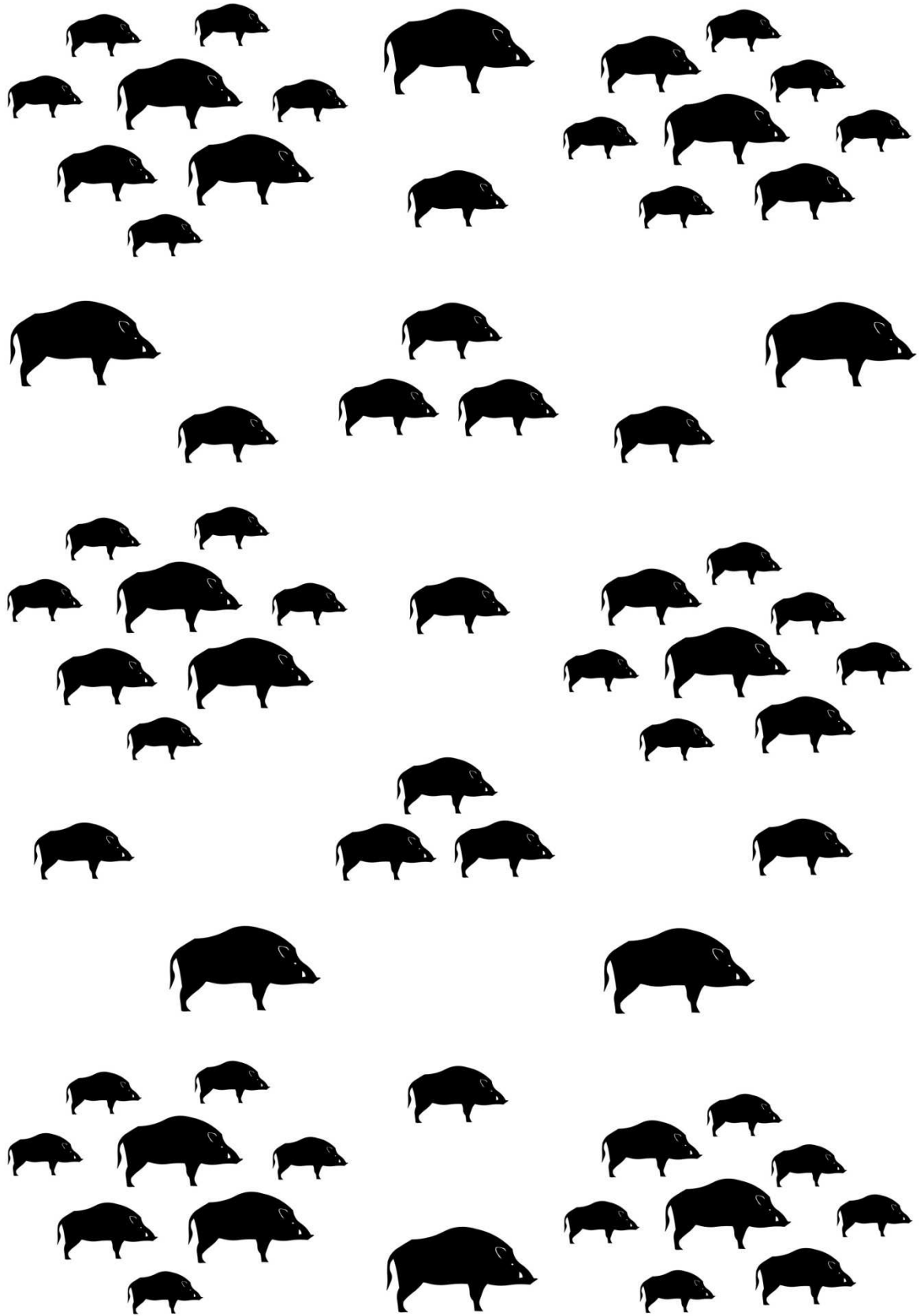
The main goal of this study, conducted in Białowieża Primeval Forest in 2007-2011, was to explore spatial and temporal patterns of social interactions in the wild boar population, and determine the role of relatedness in shaping the emergent social structure of the species. I used a combination of behavioural (trapping and telemetry) and genetic (microsatellite DNA) data to investigate group structure and composition, dispersal patterns, and population structure. Network techniques, association analyses, and estimates of lagged association rates were used to determine temporal and spatial structure of the social interactions in the study population.

Specifically, aims of the study were to:

- describe demographic composition, genetic structure and spatial relationships of wild boar groups,
- analyse spatial genetic structure of the wild boar population to infer on its social organisation,
- investigate dispersal on an individual and population levels using combination of behavioural and genetic data,
- determine temporal and spatial structure of the social interactions using association analysis and network approach,
- examine the role of relatedness and spatial relationships between individuals in shaping association patterns and social network structure,
- explore the effect of sex and age on individual's connectivity within the network.

Assuming matrilineal social structure in wild boar population, I hypothesised that:

- composition of social units will be dominated by multi-generational association of females,
- individuals of the same social units will be more related to each other than population background owing to the cross-generational site fidelity,
- females will be philopatric and dispersal will be male-biased,
- consequently, there will be a negative relationship between genetic structure and spatial distance among individuals, particularly in females, due to local increases of relatedness. At the same time a positive correlation between relatedness and strength of social bonds (i.e. associations) should be observed.
- the social network of the population will be divided into kin-clusters corresponding to matrilineal lines.





### 3. METHODS AND MATERIAL

#### 3.1. Study area

The study was conducted at two spatial scales. Firstly, a broad scale which encompassed the entire complex of the Białowieża Primeval Forest (BPF) – both Polish and Belarusian part – and its surroundings where samples for genetic analyses were collected. Secondly, a fine scale study area was located in the centre of the Polish part of the BPF where wild boar trapping, telemetry, and genetic sampling took place (Fig. 1).

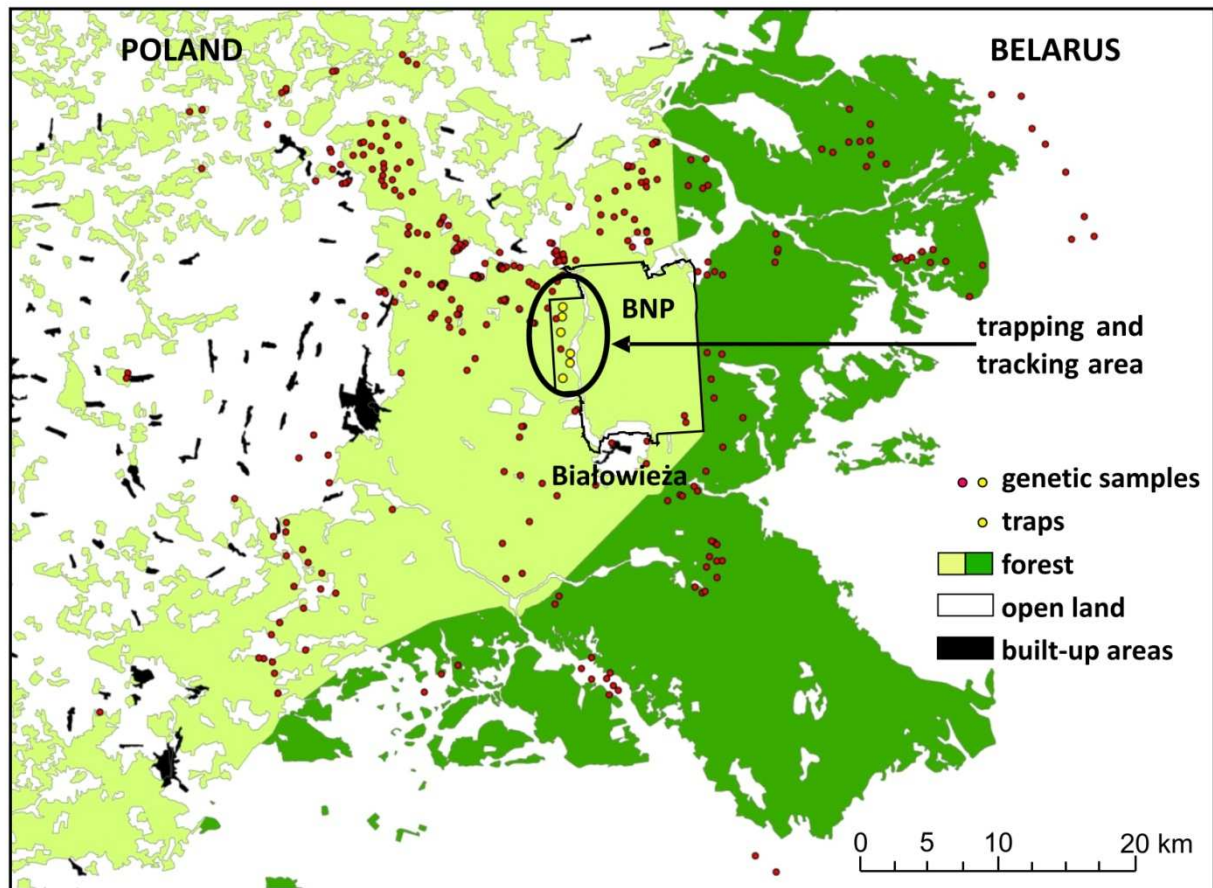


Fig. 1. Map showing the two spatial scales of the study: large area, covering entire complex of the Białowieża Primeval Forest and its surroundings, where genetic samples were collected and small area (ellipse) located in the centre of the Polish part of the BPF where trapping and telemetry took place.

The BPF is a forest complex of 1,450 km<sup>2</sup> (52°30'-53°00'N, 23°30'-24°15'E) that straddles the Polish-Belarusian border and is surrounded by a mosaic of forest and agricultural fields. It is a temperate mixed lowland forest characterised by a high share of natural stands and old-growths (Faliński 1986, Jędrzejewska et al. 1997). Most of the Polish side of the BPF (83%) is managed by the State Forestry, while the rest comprises the Białowieża National Park (BNP).

The protection of the BPF dates back to the 14<sup>th</sup> century when it became a royal hunting forest (Samojlik 2006). Thanks to this particular status, BPF has remained the last example of the European temperate lowland forest up to date. The BNP was established in 1921 to protect 50 km<sup>2</sup> area of the best preserved old-growths. In 1996, the BNP was expanded to cover 105 km<sup>2</sup>. Within the BNP, hunting and logging is prohibited, and motorised traffic is allowed only in peripheral parts of the BNP and under permission from the BNP administration. Tourists are restricted to day hikes on designated trails and overnight camping is prohibited. Within the commercial part of the BPF, limited logging and hunting occur. However, hunting from fixed locations is only permitted at a few designated sites. Motorised traffic in the commercial part of the BPF is allowed only for forestry service vehicles. Since 2011, hunting has been banned within approx. 1 km buffer zone around the border of the BNP. Additionally, there is a number of nature reserves (total area of 120 km<sup>2</sup>) with partial or strict protection scattered over the managed part of the BPF (Wesołowski 2005). The Belarusian part of the forest (860 km<sup>2</sup>) has been partially protected since 1945 and entirely as a National Park since 1991, although limited timber exploitation and hunting is permitted. Human density in the Polish part of the BPF is about 7 inhabitants/km<sup>2</sup> and the density of roads accessible for 2-wheel-drive is about 1.2 km/km<sup>2</sup> in the commercial part of the forest (Theuerkauf et al. 2003).

The climate is transitional between Atlantic and continental types, with stronger influence of the latter (Jędrzejewska and Jędrzejewski 1998). Mean number of days with snow cover is 105 (Institute of Soil Science and Plant Cultivation, <http://www.zazi.iung.pulawy.pl/>). Annual precipitation ranges from 550 to 600 mm (Institute of Geography and Spatial Planning, Polish Academy of Sciences, <http://www.igipz.pan.pl/>). During the study period, mean temperature of January and July was - 9.1°C and 21.3°C, respectively (Appendix 1).

Sixteen forest communities have been distinguished in the Polish part of BPF (Kwiatkowski 1994). Originally, a rich deciduous oak-lime-hornbeam forest stands (*Quercus robur*, *Tilia cordata*, *Carpinus betulus*; Photo 1) with admixtures of maple *Acer platanoides* and spruce *Picea abies* constituted the majority of the forest, but today this habitat is largely restricted to the protected areas. The managed part is now dominated by mixed-coniferous forests composed of Scots' pine *Pinus silvestris* and spruce with admixture of oak. Other common associations in BPF include bog alder *Alnus glutinosa* stands in wet areas with stagnating water, and ash *Fraxinus excelsior* – alder forests associated with the banks of forest rivers and creeks (Photo 1). More information about the vegetation and forest structure of the BPF can be found in Faliński (1986), Kwiatkowski (1994), and Jędrzejewska et al. (1994).

a)



b)



c)



Photo 1. Three main types of forest in the study area: a) oak-lime-hornbeam forest, b) mixed-coniferous forest, and c) ash-alder wet forest. Photos by T. Podgórski.

The BPF is unique among other European woodlands due to high tree diversity (26 tree and 55 shrub species constituting a mosaic of tree communities), a multi-storey profile of stands, relatively large amount of dead wood and outstanding diversity of flora and fauna (Faliński 1986, Wesołowski 2005).

Wild boar population within the BPF is largely shaped by natural factors (Jędrzejewska et al. 1997). Long-term dynamics of wild boar densities is primarily affected by mean annual temperature (positive effect) and, to lesser extent, wolf density (negative effect). Population growth rate is positively correlated with acorn crop of the preceding year and mean annual temperature. Density dependent interspecific competition negatively affects increase rate of the wild boar population (Jędrzejewska et al. 1997). Winter severity (depth and duration of snow cover) can cause marked decline of boar numbers and suppress reproduction in the following year. Diseases and starvation are responsible for most (73%) of natural mortality (Jędrzejewska et al. 1997, Jędrzejewska and Jędrzejewski 1998).

Two large carnivores, Eurasian lynx *Lynx lynx* and wolf occur in stable populations within the BPF (Jędrzejewska and Jędrzejewski 1998). During the study period, densities of wolf and lynx were estimated at 4 and 3 inds/100 km<sup>2</sup>, respectively (unpublished data of the Mammal Research Institute, Polish Academy of Sciences). Wild boar is predated by wolf (19% of natural mortality) and very occasionally by lynx (1%) (Jędrzejewska and Jędrzejewski 1998). The biggest wolf predation impact is on the youngest cohorts, juveniles and yearlings (70% of all wild boar killed by wolves) (Jędrzejewski et al. 2000). When natural and man-related mortality is combined, hunting, occurring in the commercial part of the BPF, appears to be the most important mortality factor (56%) (Jędrzejewska and Jędrzejewski 1998). In 2008-2011, the density of wild boar in the central part of the BPF was estimated at approx. 4 inds/km<sup>2</sup> (unpublished data of the Mammal Research Institute, Polish Academy of Sciences). The densities ranged from 3.3 inds/ km<sup>2</sup> in 2010/2011 to 5.5 in 2008/2009 (Appendix 1). Within the managed part of the BPF, average hunting harvest was 0.9 ind./km<sup>2</sup> (Regional Directorate of State Forests, Białystok). Acorn crop differed substantially between the years of the study (2008: 12 acorns/m<sup>2</sup>, 2009: 35 acorns/m<sup>2</sup>, 2010: 7 acorns/m<sup>2</sup>, 2011: 32 acorns/m<sup>2</sup>; author's unpublished data). However, long-term dynamics of acorn crop (Jędrzejewska and Jędrzejewski 1998, B. Jędrzejewska, unpublished data) suggests that mast year did not occur during the study period. In addition to wild boar, four other ungulate species occur in the forest: red deer *Cervus elaphus*, roe deer *Capreolus capreolus*, moose *Alces alces*, and the European bison *Bison bonasus*.

The study area where trapping and telemetry took place was located in the centre of the Polish part of the BPF (see Fig.1). The area consisted mainly of oak-lime-hornbeam forest

stands with a high share of old-growths and diverse forest structure (Photo 1). Additionally, ash-alder and bog alder stands were common near water courses. Mixed-coniferous stands occurred in the northern part of the trapping study area. Two-thirds of the study area (including all trapping locations) was within the borders of the BNP. The remaining part of the study area, where some animals were located temporarily, was within the commercial part of the BPF.

## **3.2. Data collection**

### ***3.2.1. Trapping and telemetry of wild boar***

Trapping was conducted every winter (November – March) from 2006/2007 to 2010/2011. Two methods were used to capture wild boar: large drop-net traps (Jędrzejewski and Kamler 2004; Photo 2) and cage traps (1.5 × 1 × 2 m) (Photo 3), both baited with maize. A combination of Zoletil (tiletamine and zolazepam) and Domitor (medetomidine) mixture (1 : 0.025 ratio) was administered intramuscularly to immobilise captured wild boar. Atipemazole hydrochloride (Antisedan) was used as an antidote (Kreeger 1997). Animals weighing less than 30 kg were only immobilised with ketamine (0.2 ml/kg) and were handled without being fully anaesthetised. Captured animals were fitted with ear tag radio-transmitters (Advanced Telemetry Systems, Isanti, Minnesota, USA and Wagener Telemetrieanlagen, Cologne, Germany) (Photo 4) and GPS collars (Vectronic Aerospace, Berlin, Germany). Skin and hair samples were collected from every captured individual. Skin samples were obtained using a standard biopsy punch. Research and handling protocol was approved by the Local Ethical Commission for Experiments on Animals in Białystok, Poland.

Upon capture, the age of wild boar was determined with 2-month interval accuracy dependent on tooth eruption (Matschke 1967). In the analyses, animals were assigned to their respective age classes during tracking period i.e. yearlings (from 6-8 to 16-18 months old), subadults (from 16-18 to 24-26 months), adults (>26 months old). Sex was determined for all individuals except two yearlings which were excluded from analyses investigating sex-related effects.

A total of 141 wild boar were captured, including 18 re-captures (at least one year after the first capture): 16 adult, 6 subadult, 31 yearling males and 32 adult, 14 subadult, 42 yearling females. Eighty-one percent (n = 114) of captured animals belonged to 16 marked groups. Group membership was established based on capture data and subsequently confirmed by telemetry data. Individuals were considered to belong to one group if they were captured together and/or were telemetrically located within 350 m distance from each other

>50% of times during 2 months following capture. The rest ( $n = 27$ ) of the animals were either solitary or belonged to unmarked groups. All animals were marked with numbered tags

Photo 2. A group of wild boar under the drop-net trap. Photo from automatic camera.



Photo 3. Solitary wild boar about to enter the cage trap. Photo from automatic camera.



Photo 4. Wild boar male fitted with radio ear-tag. Photo by T. Kamiński.



allowing for individual recognition in case of re-trapping. The proportion of individuals marked with telemetry transmitters out of all captured animals (i.e. mark rate) was 61%. Telemetry-marked animals included all solitary wild boar and on average 66% of the group's members always including all adults and subadults within the group. In total, 63 wild boars (23 males and 40 females) were marked with radio-transmitters and 12 adult wild boars with GPS-collars (6 males and 6 females).

Radio-tagged individuals were located 2-4 times per week with equal intensity during the day and night (G-test:  $G_1 = 0.48$ ,  $P = 0.49$ ). The locations of individuals were determined by recording at least 3 bearings for each triangulation using three-element Yagi antenna (Titley Scientific, Lawnton, Australia) and Yaesu FT-817 transceiver (Yaesu Musen Co., Tokyo, Japan). The location of an individual was calculated from a given set of bearings and using the maximum likelihood estimator method described by Lenth (1981). Only location estimates with error ellipse  $\leq 2$  ha were included for further analysis, and the program LOAS (Ecological Software Solutions) was used to calculate positions from triangulation. Accuracy of triangulation was determined in the field by locating transmitters in known location (Harris et al. 1990). Mean estimated error between the known transmitter location and those obtained from telemetry was  $153 \pm 9.8$  m (mean  $\pm$  SE,  $n = 120$ ). The GPS-collars recorded accurate positions of the animals every one or two hours using Global Positioning System (GPS). Location data were periodically transferred directly to the computer via GSM network or downloaded in the field via VHF wireless communication module incorporated in the collar.

Wild boars were followed for  $10.2 \pm 5.3$  months (mean  $\pm$  SD, min = 1, max = 24). On average,  $76 \pm 36$  (min = 18, max = 158) radio-locations and  $2072 \pm 1425$  (min = 337, max = 5727) GPS-locations were collected per individual.

### **3.2.2. Genetic methods**

In total, 411 wild boars were analysed using tissue ( $n = 386$ ) and hair samples ( $n = 25$ ). The majority of samples ( $n = 300$ ) were obtained from animals that were hunted or found dead (220 in the Polish and 80 in the Belarusian part of the BPF). The remaining 111 samples were collected from captured individuals. Genomic DNA was extracted using GenElute Mammalian Genomic DNA Miniprep kit (Sigma-Aldrich, St. Louis, Missouri) for tissue samples and Instagene Matrix (Bio-Rad, Hercules, California) for hair samples, and kept at  $-20^\circ\text{C}$ .

All individuals were genotyped with a panel of 16 polymorphic microsatellite loci (S090, SW72, S155, S026, S355, S215, SW951, SW857, SW24, SW122, IGF1, SW461, SW1492, SW2021, SW2496, SW2532), which had been successfully used to study

relatedness and genetic variation in wild boar populations (Vernesi et al. 2003, Iacolina et al. 2008, Scandura et al. 2008). Polymerase chain reaction (PCR) was performed in 10  $\mu$ l reaction volume, containing 3  $\mu$ l of DNA solution, 0.5 U of *Taq* DNA polymerase (Euroclone, Sizzano, Italy), 1 U PCR buffer (Euroclone), 2.5 mM MgCl<sub>2</sub>, 100  $\mu$ M of each deoxynucleosite triphosphate (dNTP), and 2 pM of each primer. The forward primer of each pair was labeled with an ABI fluorescent dye (6-FAM, HEX, or TET; Applied Biosystems, Foster City, California). The amplification profile was set up with an initial step of denaturation at 95°C for 3 min, followed by 35 cycles of 92°C for 45 s, annealing temperature (52-65°C) for 45 s, and 72°C for 30 s. A further extension step of 72°C for 10 min concluded the reaction. PCR-amplified microsatellite alleles were sized using capillary electrophoresis in an ABI PRISM 3100-Avant automatic sequencer (Applied Biosystems). Peak Scanner software (Applied Biosystems) was used to analyse electrophoretic data. Analyses were performed in the genetic laboratory of the Department of Science for Nature and Environmental Resources, University of Sassari, Italy.

### **3.3. Data analysis**

#### **3.3.1. Space use and dispersal**

Home range size was estimated with Minimum Convex Polygon (MCP) using 90% isopleth as it was recently demonstrated that using isopleths greater than 90% can result in unreliable area estimates biased by sample size and sensitive to outliers (Börger et al. 2006). Due to much higher sampling frequency of GPS-collars compared to radio-telemetry, GPS-collar data were standardised as follows: 100 locations were randomly sampled from complete GPS data set of each individual and home range size was calculated. This procedure was repeated 1000 times and resulting average home range size was assigned to a given individual.

In home range analysis, only locations (both radio and GPS) separated by at least 12 hours were chosen to ensure independence of observations (Swihart and Slade 1985). To avoid underestimation of home range size, only those individuals tracked for  $\geq 5$  months and which yielded  $>30$  locations were used in calculations of home range size ( $n = 63$ ). Using this threshold no effect of increased tracking time or number of locations on home range size was found (Spearman's  $r = 0.09$ ,  $P = 0.52$  and  $r = 0.24$ ,  $P = 0.08$ , respectively).

A general linear mixed-effects model (Pinheiro and Bates 2000) was used to investigate effect of sex and age of the individual on home range size. Mixed models were used because of the non-independent nature of the data. Group and individual identity were treated as random factors to control for social group effect and re-trapping cases. The



distribution of model residuals was checked for normality using the Shapiro-Wilk test. Home range size data were log-transformed to improve normality and reduce skewness.

Spatial overlap between areas utilised by two individuals was estimated using volume of intersection (VI) index (Kernohan et al. 2001, Fieberg and Kochanny 2005). The method measures similarity of two kernel utilisation distributions (UD) and its advantage over area-based measures is that it compares not only area shared but also intensity of use (Fieberg and Kochanny 2005). The VI index ranges between 0 (no overlap) to 1 (identical UD). The parameters used to calculate kernel UD for all animals were: bandwidth  $h = 250$  and grid size 200 based on visual assessment. Spatial overlap was used to control for spatial proximity when correlating association strength with genetic relatedness and to compare space shared among animals forming social units.

Dispersal patterns of wild boar were analysed with a combination of genetic and spatial data. Dispersal was defined as emigration by an animal from its natal area to another area where it might reproduce (natal dispersal *sensu* Howard 1960). Spatial data (radio-locations) was used to analyse temporal variation in the geographic distance of yearling and subadult wild boar (11 males, 9 females) to the centre of the natal home range. Dispersal was defined to occur when individual left its maternal home range without ever returning and the moment it had happened was the age at dispersal (Sweaner et al. 2000). In case of dispersers, average distance to natal home range centre during the last month of tracking was considered as dispersal distance. Return information on shooting location from hunters was used as last location record in case of 4 animals (2 males, 2 females).

All spatial and home-range analyses were conducted using R version 2.13.1 software (R Development Core Team 2011) and visualised in Arc View GIS 9.1 (ESRI, Redlands, California). All statistical analyses were conducted using R version 2.13.1 software (R Development Core Team 2011).

### ***3.3.2. Association patterns and network analysis***

Association analysis was based on radio-telemetry data collected in 2008 and 2009 (Table 1). The two years were treated separately due to not fully overlapping sets of marked animals. Two individuals were defined as being associated if they were located within 350 m distance from each other. The rather conservative threshold of 350 m was set to include all potential associations taking into account radio-tracking error (153-m radius around estimated location). Only simultaneous locations (collected within 1 hour) were used to define dyadic associations. High frequency sampling of GPS-collared wild boar showed that average straight-line distance covered by an animal within one hour was 33 m. The study area was

surveyed 2-4 times per week and every time an attempt to locate all marked animals was made. Only individuals located more than ten times were included in the analysis (Table 1).

Table 1. Summary of the data used to construct social networks of wild boar in 2008 and 2009.

Sex/age class of animals	N individuals	
	2008	2009
<b>Males</b>		
Yearling	6	1
Subadult	-	8
Adult	4	3
<b>Females</b>		
Yearling	9	-
Subadult	-	8
Adult	11	10
<b>N locations/ind.</b>		
Mean (SE)	60 (4)	45 (4)
Range	20 - 98	11 - 94
Median	60	41

The strength of dyadic associations was calculated using the half-weight index (Cairns and Schwager 1987):  $HWI = X/[X + 0.5(A_t + B_t)]$ , where  $X$  is the number of times individuals  $A$  and  $B$  were located together, and  $A_t$  and  $B_t$  are the total number of times individuals  $A$  and  $B$  were located. The HWI ranges between 0 (two individuals never located together) and 1 (two individuals always located together) and takes into account heterogeneity of sampling. The sampling period was set to 1 day to mirror the actual sampling schedule. An association indices matrix for each year of the study was built using SOCPROG 2.4 (Whitehead 2009) in MatLab 7.7.0 (The Mathworks Inc., Natick, Minnesota, USA). Consequently, two networks of 31 (year 2008) and 30 (2009) interconnected animals were constructed and visualised in NETDRAW (Borgatti 2002). To test whether the observed association patterns differed from random (i.e. if preferred and/or avoided associations occurred), the association data were randomly permuted 1000 times and mean HWI and its coefficient of variation (CV) were compared between real and randomised data sets (Manly

1997, Bejder et al. 1998, Whitehead et al. 2005). A significantly higher CV of real association indices compared to randomised data indicates the presence of long-term preferred companions in the population (Whitehead 1999). The procedure was repeated several times to ensure stable P values. Sexual assortativity within the networks was assessed by correlating HWI matrices with sex similarity matrices (0 – same sex, 1 – different sex) using Mantel test with 10 000 permutations to assess significance.

The wild boar social network structure was examined using modularity matrix clustering (Newman 2006, Lusseau et al. 2008). The method finds optimal network structure through iterative process of dividing the network into number of clusters from one to  $n$ , where  $n$  is the number of individuals forming the network. At each step, the number of edges (connections) within and between clusters is being quantified by modularity index  $Q$ . The most parsimonious division in the network is subsequently determined by choosing the one maximising  $Q$ , i.e. providing the most edges within clusters and the least between. Network structure analysis was performed in SOCPROG and visualised with NETDRAW. Next, genetic relatedness and spatial overlap within and between clusters (social units) of the resulting social network structure (determined by  $Q_{\max}$ ) were compared with randomisation tests using 10 000 permutations to assess significance.

### ***3.3.3. Temporal variation in associations***

All available telemetry data (radio and GPS) were used to analyse temporal stability of social relationships using previously described definition of association. The lagged association rate (LAR) and standardised lagged association rate (SLAR) (Whitehead 1995) were used to model the temporal nature of associations in the overall population and specifically for relationships within and between sex/age classes. Those techniques provide a way to quantify the proportion and duration of short and long-term associations occurring in the population by calculating the probability that a pair of individuals recorded together at time zero will still be together at subsequent time periods, and averaging it over all associations. The SLAR, as opposed to the LAR, is suitable when not all associates are recorded on every monitoring session, i.e. sampling period (Whitehead 1995). Such a sampling heterogeneity characterised radio-telemetry data which required locating animals in the field by the researcher. Consequently, temporal association patterns of radio-followed animals ( $n = 53$ ) were analysed using SLAR. In contrast, GPS-telemetry ensures uniform sampling (the GPS-collar is self-locating at fixed time intervals) and therefore LAR was used to analyse data from animals fitted with GPS-collars. Thus, the LAR analysis was restricted to adults only ( $n = 12$ ). Each LAR and SLAR was compared to the null association rate,

expected if preferential associations do not occur. The uncertainty around the lagged association rates was estimated with jackknifing procedure over 10-day periods (Whitehead 1995).

A set of mathematical models approximating features of various social structures were fitted to the observed lagged association rates (Whitehead 1995). The models utilise exponential decay and are composed of one, all, or any meaningful combination of three main components. These components are: constant companionships (permanent relationships lasting until death), casual acquaintances (associations lasting from few days to few years), and rapid disassociations (associations lasting few hours at most). In the case of LARs, eight social structure models were tested ranging from population including only constant companions (in which the association rate remains constant through time) to models describing two levels of casual acquaintances (short- and long-term). In contrast to LARs, four models consisting of two components or their combinations (constant companionships and casual acquaintances) were fitted to the observed SLARs. For formulation of the models fitted to LARs and SLARs see Appendix 2. The best fitting and most parsimonious model was selected using quasi-Akaike Information Criterion corrected for small sample size (qAIC<sub>c</sub>, Burnham and Anderson 2002, Whitehead 2007). The error around the model parameters approximating proportion and duration of different types of associations in the population was estimated using jackknifing. All analyses of the temporal association patterns were carried out in SOCPROG 2.4 (Whitehead 2009).

#### **3.3.4. Variation in sociality**

Three individual-based network measures (i.e. centrality measures: strength, eigenvector centrality, and clustering coefficient) were calculated to investigate differences in centrality (position and connectivity within the network) between individuals of different sex and age. These measures were calculated for the 2008 and 2009 networks based on half-weight association index (HWI) matrix using SOCPROG and definitions given by Whitehead (2009). Strength is a measure of gregariousness and is the sum of edges weights (i.e. association indices) connected to an individual. An individual can have high strength either because it associates weakly with many individuals or strongly with just a few. Eigenvector centrality integrates strength of a given individual and its neighbours (associates) and measures how well an individual is connected within the network. Thus, high eigenvector centrality values may result from high strength of the individual or/and its neighbours. The clustering coefficient is the proportion of an individual's neighbours that are themselves neighbours and thus describes how well associates of the focal individual are interconnected.

Clustering coefficient ranges from 0 (none of the individual's associates are connected; expected if no social grouping occurs) to 1 (all of the individual's associates are connected; expected when tight, closed social units occur).

To assess how sex and age determined sociality of individuals, generalized mixed-effects models (Pinheiro and Bates 2000, Zuur et al. 2009) were used. Three sets of models (one for each centrality measure) were built, each containing candidate explanatory variables introduced as factors: sex, age class (yearling, subadult, and adult) and interaction between them. Group, individual, and network (= year) identity were treated as random factors to control for social group effect and repeated measurements of the same individuals in two analysed years. The log-likelihood tests revealed that random effect of the network (year) was non-significant ( $P = 0.99$ ) in the model for clustering coefficient and therefore it was omitted in the saturated model for this parameter. The models were ranked according to Akaike Information Criterion corrected for small sample size ( $AIC_c$ ; Burnham and Anderson 2002).

### 3.3.5. Genetic data analysis

Basic parameters of microsatellite polymorphism and genetic diversity (number of alleles, allelic richness, expected and observed heterozygosities) were calculated using GENALEX 6.4 (Peakall and Smouse 2006) and FSTAT (Goudet 1995). GENEPOP 4.0 (Raymond and Rousset 1995) was used to estimate inbreeding coefficient ( $F_{IS}$ ) and test loci for departures from linkage equilibrium and Hardy-Weinberg equilibrium (HWE) using Markov chain method (parameters: 5000 dememorisation steps, 100 batches, 1000 iterations/batch). The significance level was adjusted for multiple testing across loci using the sequential Bonferroni correction (Rice 1989).

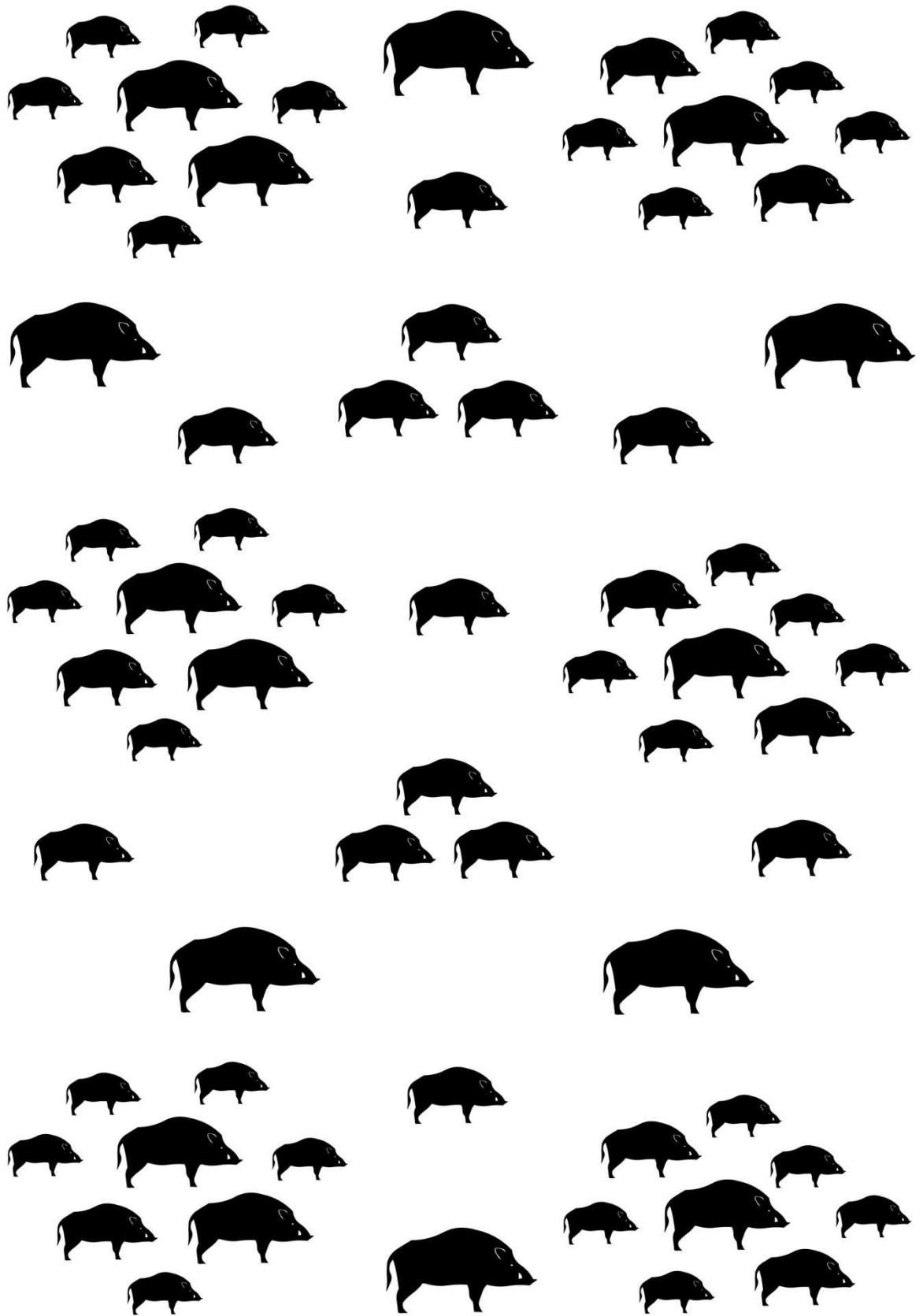
Pairwise genetic relatedness, as defined by Queller and Godnight (1989), among all sampled individuals ( $n = 411$ ) was obtained with GENALEX 6.4. These values, representing relatedness estimates based on the total allele frequencies in the population, were used in all subsequent analyses. Using total allele frequencies from the studied population, 40 reference families (40 "females", 4 "piglets/female") were simulated in KINGROUP 2 programme (Konovalov et al. 2004) to test hypotheses of kinship in wild boar groups. Additionally, maternity within the groups was established by direct comparison of genotypes allowing allele mismatch at one locus only.

Fine-scale genetic structure of the population was assessed using a spatial autocorrelation utilising permutation procedures (Smouse and Peakall 1999) as implemented in GENALEX 6.4. Autocorrelation coefficients ( $r$ ) between pairwise genetic and geographic distance matrices were calculated for variable Euclidean distance classes ranging from 1 to 60

km. The hypothesis of no spatial genetic structure was tested by 10 000 permutations of the combined data set and 10 000 bootstraps was used to estimate 95% confidence intervals around  $r$  within each distance class. Additionally, the relationship between genetic relatedness and geographic distance was analysed with Mantel test (Mantel 1967). The significance of the correlation coefficient was assessed with 10 000 random permutations (Schnell et al. 1985, Manly 1997) in GENALEX 6.4.

Two complementary methods were used to analyse the extent of sex-biased dispersal. Only adult individuals were analysed to capture post-dispersal situation. First, spatial genetic autocorrelation analysis was performed for both sexes separately. Second, assignment tests (mean corrected assignment index  $AI_c$  and its variance) were calculated separately for males and females (Goudet et al. 2002, Hammond et al. 2006) as implemented in FSTAT (Goudet 1995). Statistical significance of P-value was obtained with 10 000 randomisations. Individuals with a higher probability of being immigrants are expected to have negative values of  $AI_c$ , whereas positive  $AI_c$  values characterise individuals originating from the sampled population (Mossman and Waser 1999). The  $AI_c$  variance is expected to be larger in dispersing sex (Lawson Handley and Perrin 2007).

A correlation between social associations and genetic relatedness was analysed using Mantel tests and partial Mantel tests (Smouse et al. 1986) controlling for spatial proximity, between the association index (HWI) matrix and the corresponding matrix of pairwise relatedness estimates. The significance of all correlations was assessed using 10 000 random permutations in SOCPROG.



## 4. RESULTS

### 4.1. Social and spatial characteristics of the wild boar population

In total, 141 wild boars of known sex were captured, the majority of which (114) belonged to 16 groups. The rest of the animals were either solitary or belonged to unmarked groups. Table 2 summarises the age and sex structure of the captured individuals. Yearlings was the most common class of individuals (52% of the sample), followed by adults (34%), and subadults (14%). Overall, sex ratio tended to be slightly female biased (53 males : 88 females, Fisher's exact test:  $P = 0.054$ , testing hypothesis of 1:1 sex ratio). A similar pattern was observed in all age classes: yearlings (31 males : 42 females,  $P = 0.51$ ), subadults (6 males : 14 females,  $P = 0.33$ ), and adults (16 males : 32 females,  $P = 0.15$ ).

Groups were dominated by females (36 males : 78 females,  $P = 0.007$ ). However, significant female-biased sex ratio was observed only in adults associated in groups (2 males : 23 females,  $P = 0.001$ ). The other age classes showed even sex ratio (yearlings: 29 males : 41 females,  $P = 0.40$ ; subadults: 5 males : 14 females,  $P = 0.31$ ). The majority of adult males (88%) were solitary, whereas most of adult females (72%) remained associated in groups (Fisher's exact test,  $P < 0.001$ ). Eighty-five percent of solitary animals were adults (Table 2).

Home range size estimates were available for 63 individuals of all sex and age classes followed in 2007-2011 (Table 3, Appendix 3). Home range estimates for individuals that changed age class when re-trapped ( $n = 8$ ) were analysed separately. The size of home range (MCP 90%) averaged  $3.34 \pm 0.36 \text{ km}^2$  (mean  $\pm$  SE) (Table 3). Both, the largest and the smallest ranges were occupied by females (yearlings and subadults, respectively) (Table 3). The size of the home range was affected by an individual's age (Table 4). In fact, the mean size of the subadults' home ranges was one-third the size of other age classes' (29% of the yearlings' and 33% of the adults'), whereas yearlings and adults occupied areas of similar size (Tables 3 and 4). This pattern was uniform among sexes as indicated by non-significant interaction term of the model (Table 4). There was no sex-related difference in the size of home range (Tables 3 and 4).



Table 2. Composition of the sample of 141 wild boar captured in BPF in 2007-2011 including individuals associated in 16 groups and solitary ones. N ind. refers to the number of individuals in each category and % of sample gives proportion of the total number of captured animals. Sex-ratio of adults was calculated only for groups with  $\geq 2$  adults. Yearling: from 6-8 to 16-18 months old, subadult: from 16-18 to 24-26 months, adult:  $>26$  months old.

Category	N inds	% of sample	Group composition		
			Mean (SE)	Range	Median
<b>Groups</b>	114	80.8			
Males	36	25.5			
Adult	2	1.4	0.1 (0.08)	0 - 1	0
Subadult	5	3.5	0.3 (0.15)	0 - 2	0
Yearling	29	20.6	1.8 (0.48)	0 - 6	1.5
Females	78	55.3			
Adult	23	16.3	1.4 (0.22)	0 - 3	1
Subadult	14	9.9	0.9 (0.40)	0 - 5	0
Yearling	41	29.1	2.6 (0.66)	0 - 10	2
Group size					
Adults only			1.79 (0.20)	1 - 3	2
All age classes			7.19 (0.90)	2 - 15	6.5
Sex ratio (% of males)					
Adults only			10% (7)	0 - 50	0
All age classes			27% (5)	0 - 50	32
<b>Non-group</b>	27	19.2			
Males	17	12.0			
Adult	14	9.9			
Subadult	1	0.7			
Yearling	2	1.4			
Females	10	7.0			
Adult	9	6.3			
Subadult	0	0			
Yearling	1	0.7			
Sex ratio (% of males)					
Adults only			61%		
All age classes			63%		

Table 3. Mean values ( $\pm$  SE) of home range size (90% MCP) of wild boar followed in 2007-2011. n – number of individuals.

Sex/age class	Home range size (km <sup>2</sup> )		
	Mean $\pm$ SE	Min - Max	n
Males			
Adult	4.29 $\pm$ 1.36	0.04 - 13.75	10
Subadult	1.34 $\pm$ 0.28	0.20 - 2.49	7
Yearling	3.86 $\pm$ 0.59	1.21 - 6.65	11
Females			
Adult	3.14 $\pm$ 0.49	0.67 - 8.86	18
Subadult	1.13 $\pm$ 0.07	0.94 - 1.31	6
Yearling	4.78 $\pm$ 1.55	0.73 - 12.44	11
All	3.34 $\pm$ 0.36	0.04 - 13.75	63

Table 4. Parameters of the general linear mixed-effects model showing effects of an individual's sex and age on the home range size (MCP 90%) of wild boar. Response variable was log-transformed. All explanatory variables were factors and estimates for factor levels are presented in relation to: sex (male), and age (yearling).

Parameter	Coefficient	SE	t-value	P-value
Intercept	0.899	0.266	3.371	0.002
Age (subadult)	-0.974	0.320	-3.039	0.005
Sex (female)	0.164	0.224	0.730	0.470
Age (adult)	-0.188	0.322	-0.584	0.563
Sex (female) $\times$ Age (subadult)	0.316	0.387	0.815	0.421
Sex (female) $\times$ Age (adult)	0.027	0.387	0.069	0.945

## 4.2. Genetic variation of the population

In total, 123 alleles were detected across 16 analysed loci. All loci were polymorphic with the number of alleles per locus ranging between 3 (S355, S215) and 15 (SW2021) in 411 genotyped individuals (Table 5). The overall inbreeding coefficient ( $F_{IS} = -0.004$ ) was not significantly different from zero indicating no deficiency or excess of heterozygotes. Averaging across loci, observed heterozygosity was moderate (mean  $\pm$  SE:  $0.568 \pm 0.068$ ) and similar to expected heterozygosity ( $0.578 \pm 0.069$ ). Deviations from HWE were observed at 2 single loci (Table 5).

Table 5. Genetic variability of 16 microsatellite loci analysed in 411 wild boar from BPF (see Fig 1. for spatial distribution of samples).  $N_a$  – observed number of alleles/locus, Allelic richness – mean number of alleles/locus over population,  $H_e$  – expected heterozygosity,  $H_o$  – observed heterozygosity, HWE (P-value) – probability of  $H_o$  given  $H_e$  (significant deviations from HWE following sequential Bonferroni correction are in bold).

Locus	$N_a$	Allelic richness	$H_e$	$H_o$	HWE (P-value)
S090	8	6.52	0.687	0.654	0.054
SW72	6	4.48	0.655	0.649	0.345
S155	8	4.56	0.470	0.513	0.589
S026	4	3.80	0.510	0.536	0.583
S355	3	2.16	0.078	0.075	0.424
S215	3	2.95	0.223	0.220	0.797
SW951	6	2.72	0.038	0.021	0.012
SW857	5	4.13	0.642	0.614	<b>&lt; 0.001</b>
SW24	8	6.32	0.524	0.496	0.049
SW122	7	6.99	0.799	0.826	0.487
IGF1	11	9.21	0.833	0.847	0.206
SW461	10	9.92	0.867	0.888	0.008
SW1492	5	4.24	0.425	0.411	0.484
SW2021	15	11.22	0.828	0.829	0.051
SW2496	13	11.35	0.858	0.678	<b>&lt; 0.001</b>
SW2532	11	9.42	0.807	0.815	0.104
Mean (SE)	7.7 (0.89)	6.25 (0.77)	0.578 (0.069)	0.568 (0.068)	

Linkage disequilibrium resulted for 10 (out of 120) loci combinations, 8 of which included markers mapped in different chromosomes, so that physical linkage could be excluded. Overall, coefficient of relatedness in the studied population averaged  $-0.002 \pm 0.001$  (mean  $\pm$  SE).

### **4.3. Socio-genetic structure of the population**

Mean pairwise genetic relatedness among trapped animals was  $0.040 \pm 0.002$  (mean  $\pm$  SE,  $n = 111$  inds). Individuals associated in groups ( $n = 15$  groups) showed a higher mean relatedness than solitary/non-associated ones (mean  $\pm$  SE;  $0.247 \pm 0.011$  and  $-0.015 \pm 0.022$ , respectively;  $P < 0.001$ ; Fig. 2a). Individuals within groups were, however, less related to each other than animals in reference, fully-related families (Fig. 2a). Consequently, levels of relatedness within adult female – yearling (Photo 5) and adult female – subadult pairs (mean  $\pm$  SE;  $0.215 \pm 0.022$  and  $0.258 \pm 0.050$ , respectively) were lower compared to mother – offspring from reference families (Fig. 2b). Similarly, mean relatedness within pairs of yearlings, subadults, and adult females associated in the groups (mean  $\pm$  SE;  $0.261 \pm 0.016$ ,  $0.366 \pm 0.037$ , and  $0.383 \pm 0.034$ , respectively) exhibited lower levels of relatedness compared to reference siblings (Fig. 2c), thus contradicting the full-sibship hypothesis.

However, parentage analysis showed that all groups except one contained at least one family, i.e. mother and offspring (73% of groups) or full siblings (20%) (Table 6). The average group contained 1.7 families (min.-max.: 0-5), members (i.e. first degree-relatives) of which made up on average 82% of individuals in the group (38-100%). Additionally, overlapping distributions of relatedness between simulated kinship classes and observed association types (Fig. 2) indicate a substantial share of highly related individuals present in the trapped groups. Therefore, it appears justified to call them family groups.

Mean intra-group relatedness decreased significantly with increasing group size (Fig. 3). This indicates that larger groups are composed of a mix of families or have admixture of unrelated individuals.

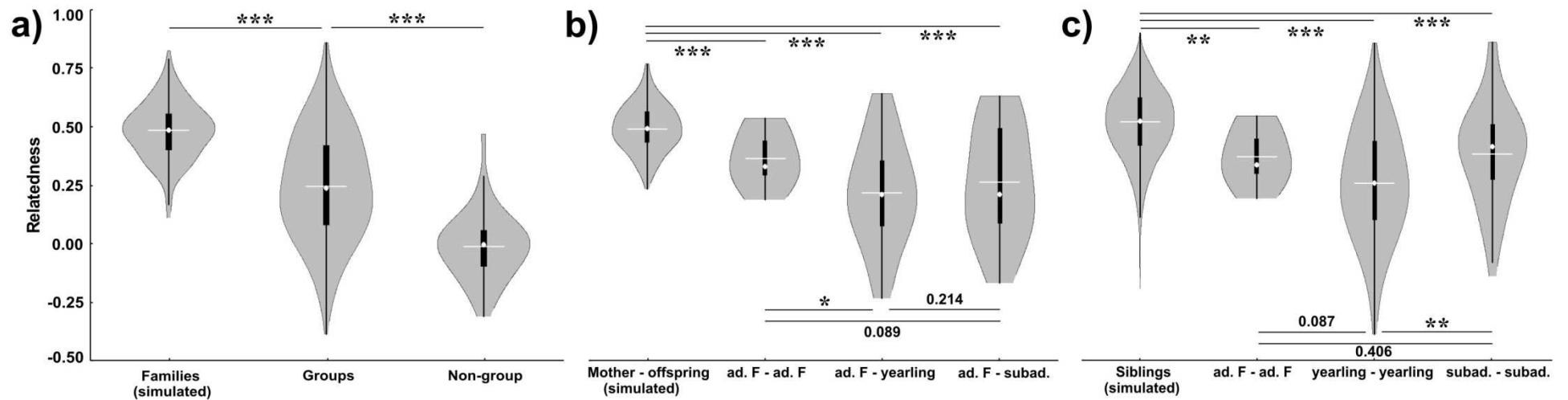


Fig. 2. Distributions of relatedness values: a) within simulated families ( $n = 400$  dyads), trapped groups ( $n = 439$ ), and animals not associated in groups ( $n = 43$ ), b) among intra-group pairs of simulated mother – offspring ( $n = 434$ ), adult female – adult female ( $n = 10$ ), adult female – yearling ( $n = 102$ ), and adult female – subadult ( $n = 22$ ), c) among intra-group simulated siblings ( $n = 7139$ ), adult female – adult female ( $n = 10$ ), yearling – yearling ( $n = 223$ ), and subadult - subadult ( $n = 40$ ). The violin plots combine box plot and density trace (smoothed histogram of the data) and embedded boxes indicate interquartile range, white circle the median, white horizontal line the mean, and black vertical lines extend to  $\pm 1.5$  times the interquartile range. Statistical significance of the differences between the means (\*\*\*)  $P < 0.001$ , \*\*  $P < 0.01$ , \*  $P < 0.05$ ) was obtained with randomisation tests (10 000 permutations).

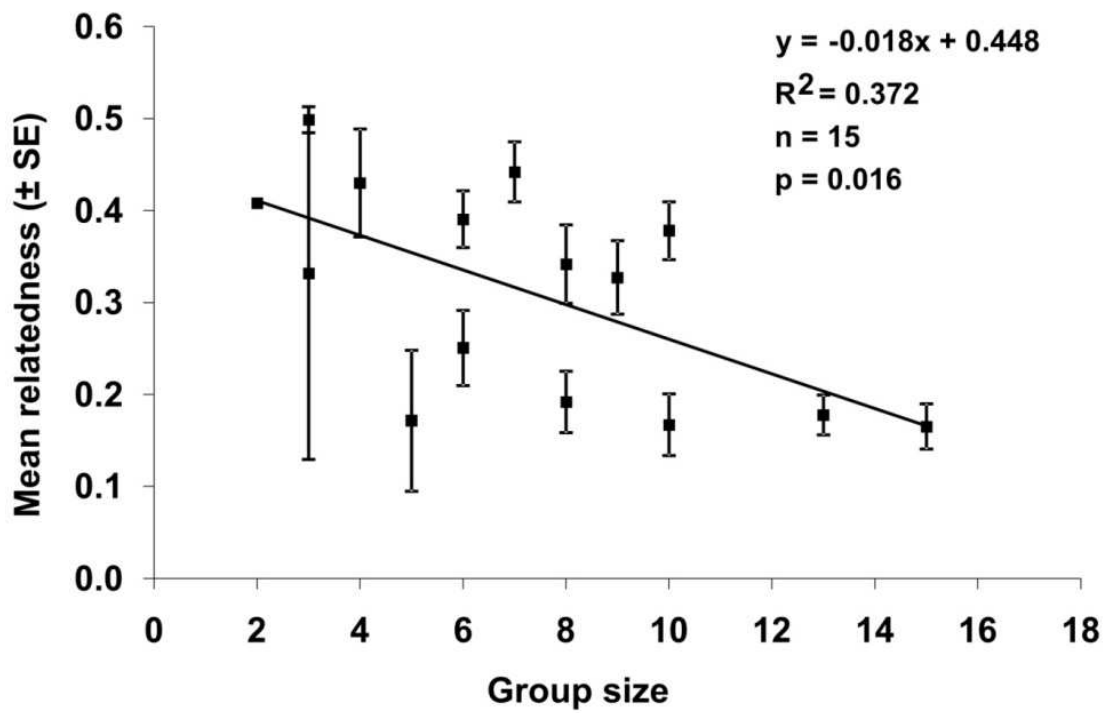


Fig. 3. Relationship between mean intra-group relatedness and size of trapped groups of wild boar (n = 15 groups).



Photo 5. Sow and yearling rooting for food in the wintertime in BPF. Photo by T. Podgórski.

Table 6. Kinship relations within captured wild boar groups (n = 15). Maternity and sibship were established by direct comparison of genotypes ( $\geq 14$  loci compared) allowing allele mismatch at one locus.

Group ID	Group size	Mother ID	N offspring	N siblings (no mother)	Unassigned
1	6	A (ad.)	4	-	1 (yearling)
2	6	A (ad.)	4	-	1 (yearling)
3	3	-	-	2 (yearlings)	1 (yearling)
4	9	A (ad.)	2	-	-
		B (ad.)	5		
5	15	A (ad.)	7	2 (yearlings)	5 (yearlings)
6	10	A (ad.)	6	2	1 (yearling)
		B (ad.)	1	(ad. females A and B)	
7	4	A (ad.)	3	-	-
8	13	A (ad.)	1	4 (2, 2) (yearlings)	-
		B (ad.)	1		
		C (ad.)	4		
9	10	A (ad.)	2	2	1 (subad. male)
		B (subad.)	3	(subad. females B and C)	
		C (subad.)	1		
10	8	A (ad.)	1	6 (subadults)	-
11	7	A (ad.)	5	2 (ad. females	-
		B (ad.)	-	A and B)	
12	2	-	-	-	2 (ad. females)
13	5	A (subad.)	2	-	2 (subadults)
14	8	A (ad.)	4	2 (ad. females	1 (yearling)
		B (ad.)	1	A and B)	
15	3	-	-	3 (ad. females)	-
Mean/group	7.3	1.3	3.8	1.8	1.0
( $\pm$ SE)	(0.96)	(0.25)	(0.68)	(0.42)	(0.34)
Range	2-15	0-3	0-7	0-6	0-5

#### 4.4. Dispersal and spatial genetic structure of the population

Dispersal patterns were determined from a combination of spatial and genetic data. Temporal variation in the geographic distance to the centre of the natal home range was analysed for 20 yearling wild boar (Fig. 4). The majority of yearlings (60%) did not disperse and the distance to the centre of the maternal range throughout the monitoring period remained similar in males (mean  $\pm$  SE: 1124  $\pm$  26 m, n = 634 locations) and females (1131  $\pm$  37 m, n = 469) (Mann-Whitney U-test: W = 156074, P = 0.152; Fig. 4). The distance to the natal home range centre maintained by non-dispersing yearlings corresponded to the radius of the average adult female home range (1000 m, Fig. 4).

Forty percent of the focal individuals dispersed (i.e. left their natal home range permanently) (Table 7). There was no evidence for sex-biased dispersal as each sex constituted half of the dispersers. However, males tended to disperse for longer distances than females (Table 7). The age at which the dispersal event occurred was similar in males and females (18-20 and 19-21 months, respectively). Interestingly, long-distance emigration was also observed in adult wild boar (> 3 years old). One adult male was hunted 28 km away from the centre of their home ranges and two adult females 28 and 30 km away (Appendix 4). The proportion of long-distance migrants in the sample of all marked adults was 5% in males and 6% in females.

Overall, the coefficient of relatedness in the studied population averaged  $-0.002 \pm 0.001$  (mean  $\pm$  SE, n = 411 inds). Pairwise genetic relatedness among individuals showed a slightly negative correlation with geographic distance within the study area (Mantel test:  $r = -0.083$ , P < 0.001, 10 000 permutations; Fig. 5).

Fine-scale spatial autocorrelation analyses indicated presence of genetic structure among adult individuals only over short distances. Correlation coefficients (r) between spatial and genetic distances had positive values significantly different from zero within 0-1 and 1-5 km distance classes only (Fig. 6). In the subsequent distance classes (5-60 km) r was no longer greater than at random. Thus, spatial genetic structure of wild boar in BPF was maintained at a distance up to 5 km.

If dispersal is dominated by one of the sexes, it is mirrored in weak and quickly disappearing genetic structure of the dispersing sex, whereas the philopatric one exhibits distinct structuring stretching over larger distances. To test this, spatial genetic structure was analysed for each sex separately and only adult individuals were considered to capture post-dispersal situation. Both, males and females showed significantly positive r-values in the distance classes up to 5 km (Fig. 6).



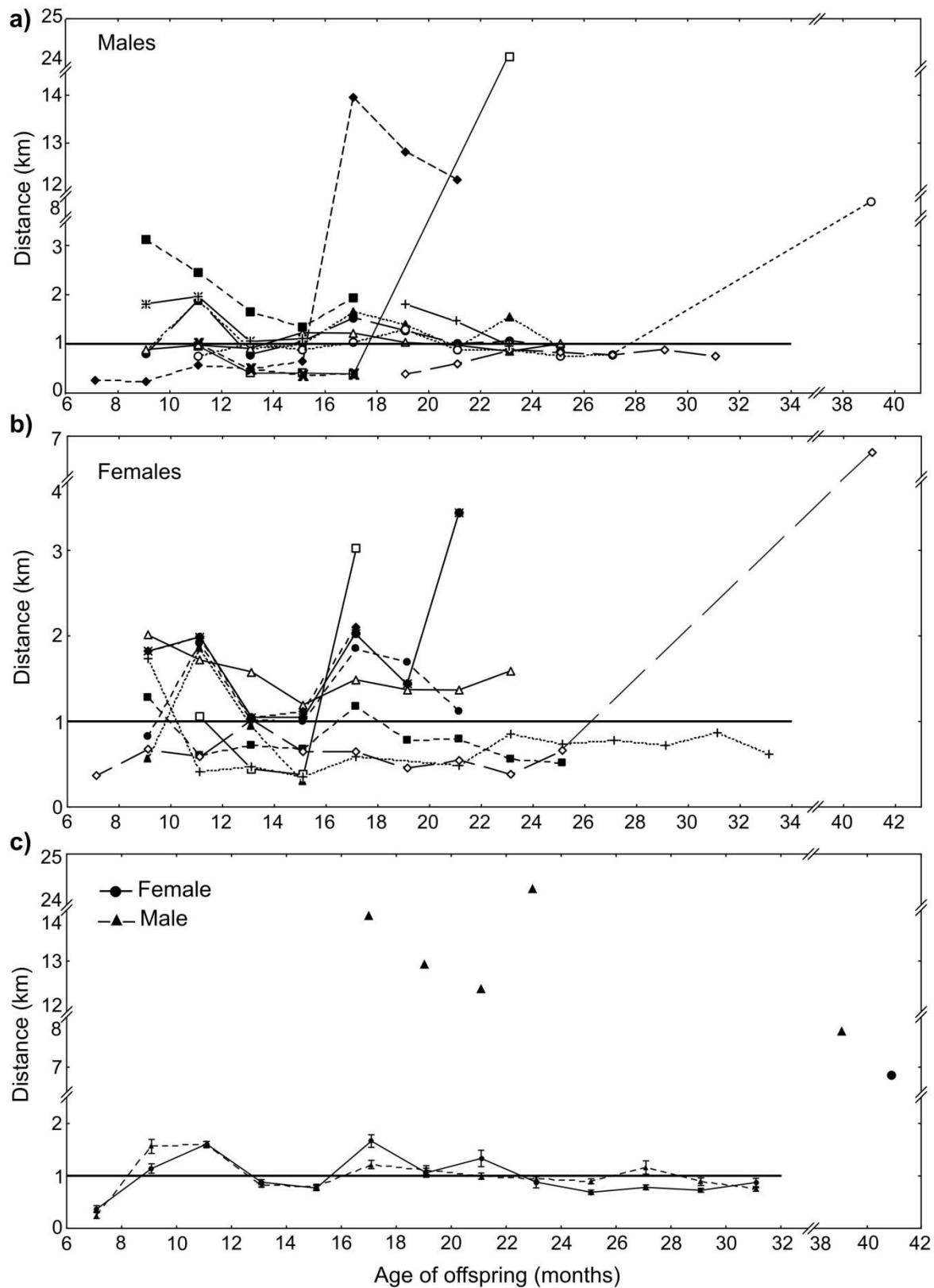


Fig. 4. Temporal variation in the individual (a and b) and average  $\pm$ SE (c) distance of male and female offspring to the centre of mother's home range (90% MCP). In a) and b) symbols represent individuals. Single points in c) indicate outliers (i.e. long-distance dispersers). Horizontal solid lines indicate a radius of average home range of adult female wild boar.

Table 7. Individual variation in dispersal parameters of 20 yearling wild boar from Białowieża Primeval Forest in years 2007-2010. The table details offspring identity (ID) and its mother identity (in parentheses), age of offspring during tracking, distance to the centre of maternal home range during the last month of following (Distance), and whether individual dispersed or not (Dispersed) (i.e. left maternal home range permanently) and at what age dispersal event occurred (in parentheses).

ID	Age during tracking (months)	Distance (meters)	Dispersed
<b>Males</b>			
8 (4)	10-12 to 16-18	390	no
45 (27)	18-20 to 30-32	741	no
22 (19)	6-8 to 24-26	913	no
10 (13)	6-8 to 24-26	931	no
12 (13)	6-8 to 24-26	959	no
47 (46)	16-18 to 22-24	978	no
59 (48)	8-10 to 14-16	1092	no
24 (25)	6-8 to 16-18	<b>1946</b>	yes (10-12)
38 (36)	22-24 to 38-40	<b>7826</b>	yes (28-38)
54 (52)	6-8 to 20-22	<b>11579</b>	yes (16-18)
7 (4)	14-16 to 22-24	<b>24195</b>	yes (18-20)
Mean dispersal distance ( $\pm$ SE)		<b>11384 (<math>\pm</math>4707)</b>	
Percent of dispersers			36%
Average dispersal age (months)			18-20
<b>Females</b>			
29 (28)	8-10 to 24-26	552	no
30 (27)	8-10 to 32-24	616	no
14 (13)	6-8 to 14-16	624	no
11 (13)	6-8 to 20-22	1171	no
61 (46)	6-8 to 16-18	1466	no
23 (25)	8-10 to 22-24	<b>1968</b>	yes (10-12)
9 (4)	8-10 to 16-18	<b>3037</b>	yes (16-18)
60 (48)	8-10 to 20-22	<b>3713</b>	yes (20-22)
32 (31)	20-22 to 40-42	<b>6795</b>	yes (28-40)
Mean dispersal distance ( $\pm$ SE)		<b>3879 (<math>\pm</math>1036)</b>	
Percent of dispersers			44%
Average dispersal age (months)			19-21

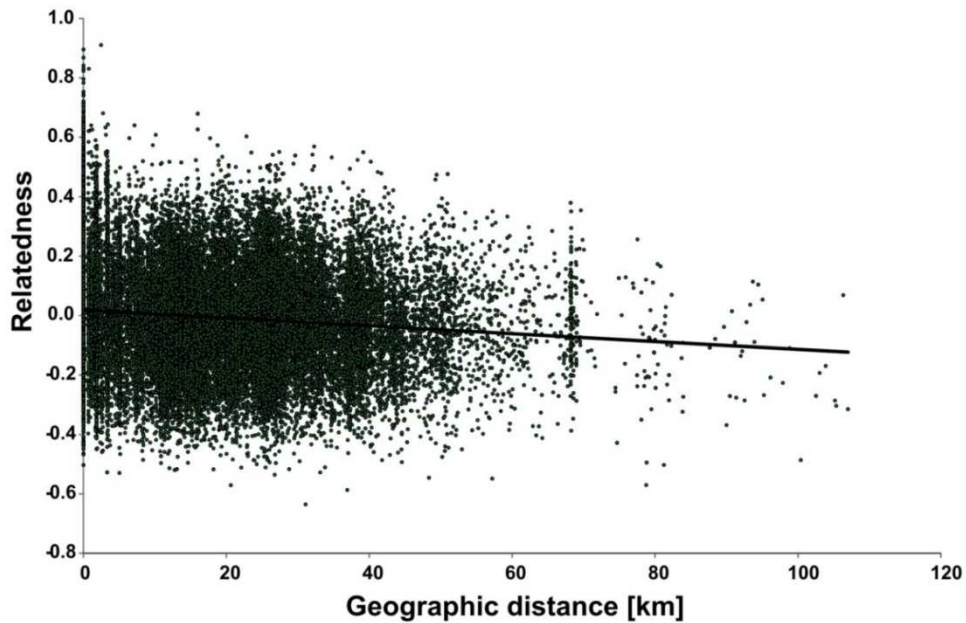


Fig. 5. Spatial correlation between geographic distance and genetic relatedness as determined by Mantel test ( $r = -0.083$ ,  $P < 0.01$ , 1000 permutations, 411 samples).

However, strength of the correlation differed between sexes depending on the distance. Within the 0-1 km distance class females had higher  $r$ -values than males (mean  $\pm$  SE:  $0.166 \pm 0.0001$  and  $0.113 \pm 0.0003$ , respectively;  $t$ -test:  $t = 154.81$ , d.f. = 14733.6,  $P < 0.001$ ), whereas within 1-5 km distances males showed  $r$ -values twice as high as females ( $0.037 \pm 0.0001$  and  $0.017 \pm 0.00001$ , respectively;  $t$ -test:  $t = 120$ , d.f. = 16090.2,  $P < 0.001$ ). This may reflect females tendency to settle in the direct neighbourhood of a kin. Nevertheless, overall similarity in structuring and its decay over geographic distance between sexes does not provide enough support for sex-biased dispersal.

Similarly, assignment index analysis provided little evidence for sex-biased dispersal. Individuals with higher probability of being immigrants are expected to have negative values of corrected assignment index ( $AI_c$ ), whereas positive  $AI_c$  values characterise individuals with a lower probability of being migrants. The 50 adult males analysed had negative mean assignment index (mean  $AI_c = -0.259$ ) in contrast to the positive mean assignment index for the 78 adult females (0.166). Additionally, males also had a greater  $AI_c$  variance (13.33) than females (12.06), suggesting higher variability due to the mixture of immigrants and native males. However, differences between sexes in both parameters were not significant ( $AI_c$ :  $P = 0.52$ ,  $AI_c$  variance:  $P = 0.79$ ). Despite marked tendency towards greater dispersal in males than in females, results of the tests for biased dispersal suggest that the bias is insignificant.

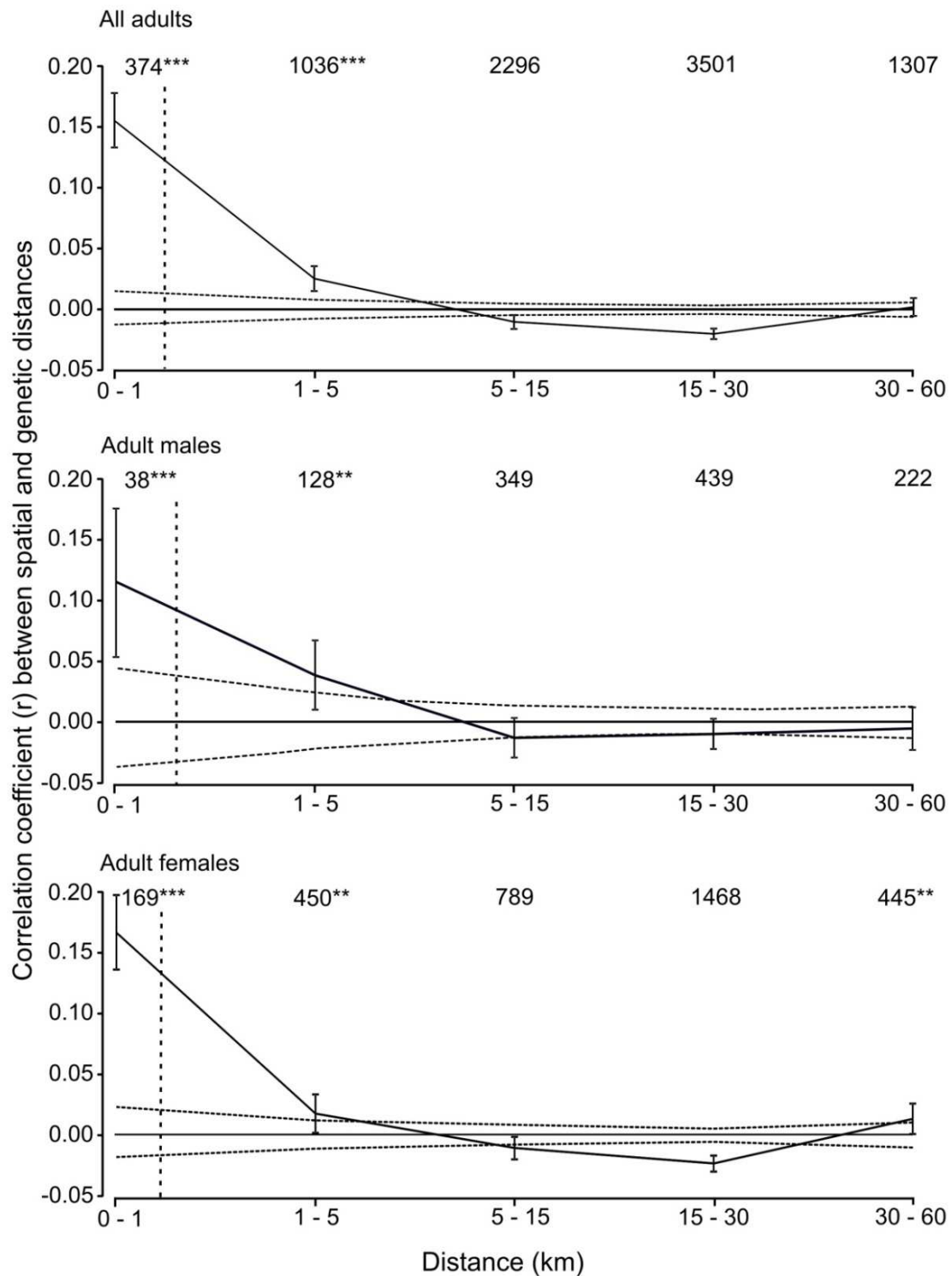


Fig. 6. Spatial genetic structure of adult wild boar in Białowieża Primeval Forest. Dashed lines represent 95% confidence interval around null hypothesis of no spatial structure as determined by permutation. Error bars (95% confidence interval around  $r$ ) were obtained by bootstrapping. The numbers of pairwise comparisons within each distance class is presented above the plotted values. Vertical broken lines represent diameter of the average home range. Asterisks indicate statistically significant positive spatial autocorrelation values (\*\*\*  $P < 0.001$ , \*\*  $P < 0.01$ ).

## 4.5. Association patterns

### 4.5.1. General characteristics

Radio-telemetry data from two years (2008: 31 animals and 2009: 30 animals) was used to investigate association patterns in wild boar population. The mean ( $\pm$ SE) half-weight association index (HWI) among all individuals was 0.095 (0.008) in 2008 and 0.068 (0.007) in 2009 indicating that two randomly chosen individuals spent on average 9.5% and 6.9% of the time together in 2008 and 2009, respectively. However, in the two analysed years, the majority of dyads did not associate (66% and 80%, respectively). The mean ( $\pm$ SE) of all nonzero HWI values was 0.277 (0.019) in 2008 and 0.336 (0.026) in 2009 suggesting that of the two years of the study, individuals that associate spent 27.7% and 33.6% of the time together, respectively. The mean ( $\pm$ SE) values of the maximum HWI (2008: 0.66 (0.05); 2009: 0.50 (0.05)) indicated that some pairs of individuals formed strong associations and remained associated for 66% and 50% of the time in 2008 and 2009, respectively. The sex of two individuals forming an association did not affect the HWI between them in the two years of the study (Mantel test; 2008:  $r = 0.022$ ,  $P = 0.39$ ,  $n = 378$ ; 2009:  $r = 0.005$ ,  $P = 0.49$ ,  $n = 435$ ) indicating no sexual segregation in social contacts.

The association dataset was randomly permuted 1000 times. The observed mean HWI was significantly lower than the random mean (2008: observed mean = 0.095, random mean = 0.104,  $P < 0.001$ ; 2009: observed mean = 0.068, random mean = 0.072,  $P < 0.001$ ) showing that individuals formed preferential associations in both years of the study. Additionally, the observed coefficient of variation of the HWI was also significantly higher than the random one (2008: observed CV = 2.54, random CV = 1.76,  $P < 0.001$ ; 2009: observed CV = 3.13, random CV = 2.44,  $P < 0.001$ ) indicating a wider variety of associations than expected by chance (i.e. presence of associations with higher and lower HWI than expected by chance). Consequently, proportion of nonzero associations in the population was significantly lower than at random (2008: observed 34%, random 91%,  $P < 0.001$ ; 2009: observed 20%, random 66%,  $P < 0.001$ ) and mean nonzero HWI was significantly higher than at random (2008: observed mean = 0.277, random mean = 0.114,  $P < 0.001$ ; 2009: observed mean = 0.336, random mean = 0.110,  $P < 0.001$ ). Altogether, the null hypothesis that the wild boar in the study population associate randomly was rejected.

#### 4.5.2. Association patterns and genetic relatedness

In both, 2008 and 2009, association strength and genetic relatedness were positively correlated. The same pattern held true when correlations were controlled for spatial overlap of utilised area (Table 8). The relationship between association strength and relatedness between individuals was stronger in 2008 and it may be attributed to higher proportion of yearlings (remaining within family groups) in the sampled animals compared to 2009 (52% and 3%, respectively). Association strength among females correlated positively with their genetic relatedness, regardless of whether or not spatial overlap was controlled for (Table 8). Contrastingly, association strength among males did not correlate with their relatedness, except for 2008 when spatial overlap was not controlled for (Table 8). This exception can be explained by a large proportion of yearlings remaining within family groups which is supported by a lack of correlation when spatial proximity was controlled for.

Table 8. Correlation coefficients between association strength (HWI – half-weight association index) and genetic relatedness (n – number of pairwise comparisons) in wild boar population. Correlation coefficients (r) and statistical significance (P) were obtained using Mantel and partial Mantel (controlling for spatial overlap of utilised area) tests based on 10 000 permutations.

Category	2008			2009		
	n	r	P	n	r	P
All	465	0.502	<0.001	435	0.243	<0.001
Females	190	0.494	<0.001	136	0.210	0.007
Males	45	0.325	0.020	78	0.131	0.134
Controlled for spatial overlap of utilised area						
All	465	0.209	<0.001	435	0.172	<0.001
Females	190	0.204	0.006	136	0.129	0.048
Males	45	-0.032	0.569	78	0.172	0.086

#### 4.6. Temporal patterns of associations

Adult wild boar formed non-random, preferential associations which, as shown by lagged association rates (LAR), were temporarily relatively stable (Fig. 7a). The LAR estimates probability that a pair of individuals recorded together at time zero will still be together at subsequent time periods, and averages it over all associations. The levels of LAR was higher than expected by chance and did not fall to null association level (i.e. LAR if individuals associated randomly). The proportions and duration of short and long-term associations occurring in the population were estimated with a set of exponential models which were fitted to the observed LARs (Fig. 7). The models are composed of one, all, or any meaningful combination of three main components: constant companionships (permanent relationships lasting until death), casual acquaintances (associations lasting from few days to few years), and rapid disassociations (associations lasting few hours at most). Table 9 and Appendix 2 detail components of the models fitted to LARs observed for all adults, as well as within and between sexes.

Interaction patterns among adults in the population were dominated by long-term relationships which lasted few years and represented 69% of the associations in the population (Table 9). Short-term, casual acquaintances lasting on average one day characterised roughly one-third of the associations (Table 9).

Adult females formed non-random, long-term associations that were stable over time (Fig. 7b). The vast majority (81%) of female-female associations were life-time long. The rest lasted for about a week (10% of associations) or disintegrated within a day (Table 9). Contrastingly, male-male and male-female relationships were more dynamic and reached the level of random association after a relatively short time (Figs 7c and 7d). Most of associations among adult males (60%) broke down within a day, 34% lasted several days, and only 6% had permanent character (Table 9). Female-male interactions were particularly short-lived: 76% of associations disintegrated within a day, 24% lasted few days and there virtually no long-lasting relationships (Table 9).

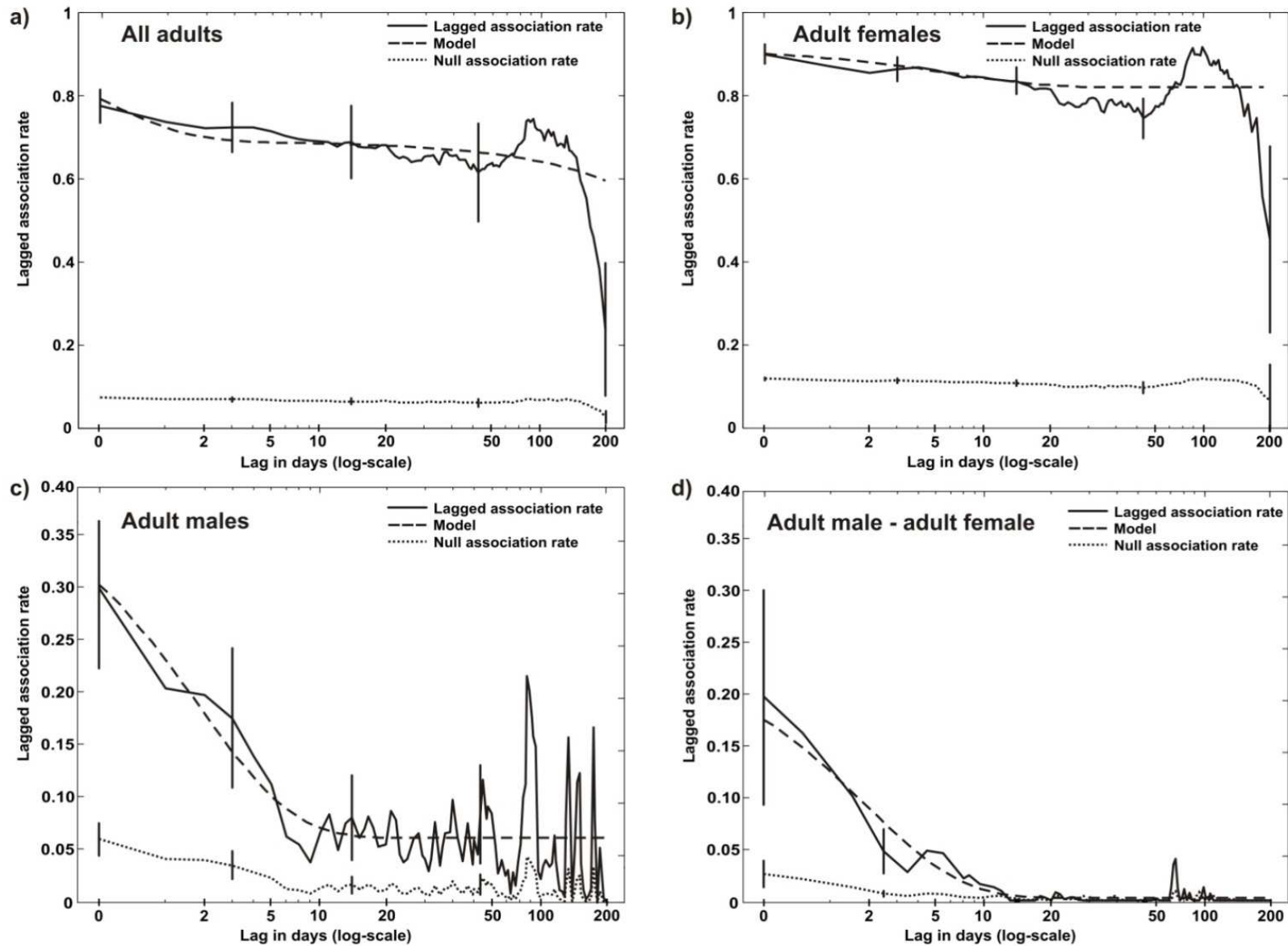


Fig. 7. Temporal patterns of associations described by lagged association rates (LARs) for: (a) all adult wild boar, (b) among adult females, (c) among adult males, and (d) between adult males and adult females in BPF. The LARs are compared to null association rates (LAR if individuals associated randomly) and the best fit model is shown for each LAR (see Table 9 for description). Standard error bars were obtained by jackknifing.



Table 9. Values and temporal characteristics of the social components derived from the models fitted to lagged association rates (LARs) among all individuals as well as within and between sexes of adult wild boar in Białowieża Primeval Forest (see Fig. 7). Each model consists of a proportion of constant companions (CC,  $p_{cc}$ ), rapid disassociations (RD), and casual acquaintances (CA) of two types: permanent acquaintances ( $p_{perm}$ ) lasting for particular period of time ( $\tau_{perm}$ ) and casual acquaintances ( $p_{ca}$ ) that last for shorter periods ( $\tau_{ca}$ ). This values correspond to percentage of each social component in the population. The standard error (SE range around the mean) of each parameter was estimated by jackknifing procedure. The best fitting model was chosen by minimising quasi-Akaike Information Criterion value (qAIC). For a more detailed description of the models see Whitehead (1995). Formulation and parameters of the models are given in Appendix 2.

Model component		Value	(SE range)
All adults			
Permanent acquaintances ( $p_{perm}$ )		69%	(60–78)
Duration of permanent acquaintances ( $\tau_{perm}$ )		3.7 years	(1.6–9.1)
Casual acquaintances ( $p_{ca}$ )		31%	(22–40)
Duration of casual acquaintances ( $\tau_{ca}$ )		0.9 days	(0.5–4.8)
Female – female			
Constant companionships ( $p_{cc}$ )		81%	(72–90)
Casual acquaintances ( $p_{ca}$ )		10%	(4–16)
Duration of casual acquaintances ( $\tau_{ca}$ )		7.1 days	(4.4–18.4)
Male – male			
Constant companionships ( $p_{cc}$ )		6%	(5–7)
Casual acquaintances ( $p_{ca}$ )		34%	(13–55)
Duration of casual acquaintances ( $\tau_{ca}$ )		2.8 days	(2.0–4.6)
Male – female			
Constant companionships ( $p_{cc}$ )		0.2%	(0–0.8)
Casual acquaintances ( $p_{ca}$ )		24%	(3–45)
Duration of casual acquaintances ( $\tau_{ca}$ )		2.9 days	(1.1–4.8)

The standardised lagged association rates (SLARs) calculated for associations among animals of all age classes, between yearlings/subadults and adults, and among yearlings/subadults were stable over time, higher than expected by chance and not falling to random association level indicating presence of preferential companionships (Fig. 8). An exponential model estimating number of associates and duration of relationships was fitted to each SLAR calculated for all animals and specific age classes (Fig. 8). However, in contrast to LARs, models fitted to SLAR's contain only two components or their combinations: constant companionships and casual acquaintances. Table 10 and Appendix 2 detail components of the models fitted to observed SLARs.

Association patterns among all animals (yearlings, subadults, and adults) were best described by the model including casual acquaintances component only. However, duration of these casual acquaintances (5.3 years) indicate that they represent relationships stable over time and long-lasting (Fig. 8a, Table 10). At a very short time lags, y-intercept of the SLAR represents reciprocal of the mean number of short-term companions of a randomly chosen individual (Whitehead 1995) which provides an approximation of the group size derived solely from social interactions. A randomly chosen individual from the population was expected to have 4-5 associates at a time (Table 10). This provides the estimated group size of 8 animals (scaled by mark rate of 61% plus one for the individual), which roughly corresponds to trapping data (mean group size  $\pm$  SD:  $7.2 \pm 3.6$ ).

The best model describing temporal patterns of associations between yearlings/subadults and adults consisted of constant, long-term companionships and short-term, casual acquaintances (Fig. 8b, Table 10). The proportion of constant companions (potentially life-time long) in the total number of association types was 83% (value of SLAR at its level-off point in relation to its maximum i.e. model line y-intercept). This corresponds to ~1 adult being constant companion of the yearling/subadult (Table 10). Short-term, casual acquaintances between yearlings/subadults and adults were estimated to last 40 days on average (Table 10).

The relationships among yearlings/subadults were best described by a model containing a casual acquaintances component only (Fig. 8b, Table 10). However, SLAR decayed very slowly over time and never reached the random level (Fig. 8b) indicating preferential and stable affiliations in those age classes (Fig. 8b). In fact, estimated duration of associations among yearlings/subadults was almost 11 years corresponding to permanent, potentially life-long relationships (Table 10).

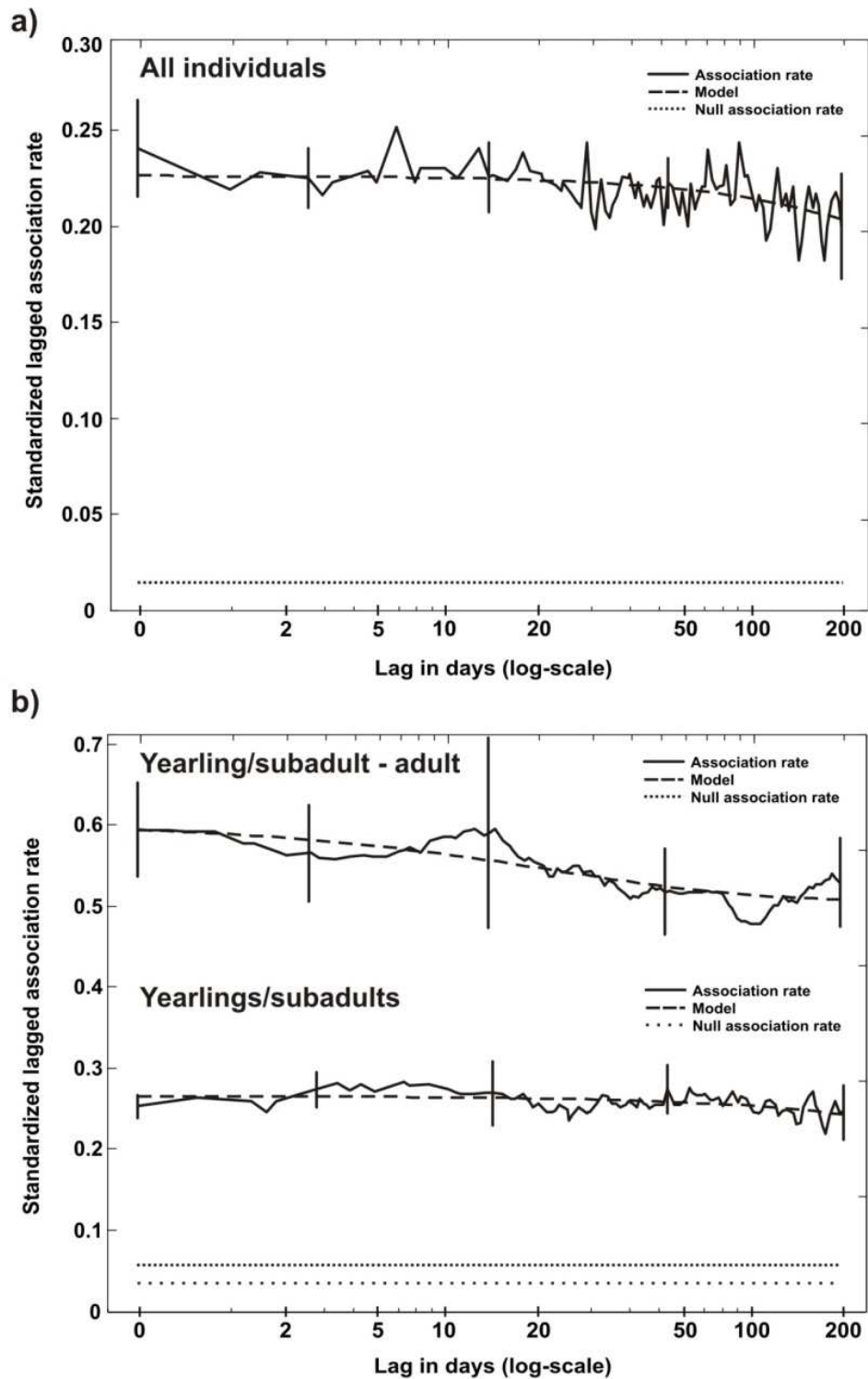


Fig. 8. Temporal patterns of associations described by standardised lagged association rates (SLARs) among all radio-marked wild boar (a) and between yearlings/subadults and among yearlings/subadults (b) in Białowieża Primeval Forest. The SLARs are compared to null association rates (SLAR if individuals associated randomly) and the best fit model is shown for each SLAR (see Table 10 for description). Standard error bars were obtained by jackknifing.

Table 10. Parameters of the social structure derived from the models fitted to standardised lagged association rate (SLAR) among all wild boar (yearlings, subadults, and adults), within yearlings/subadults, and between yearling/subadults and adults in Białowieża Primeval Forest. The standard error (SE range around the mean) of each parameter was estimated by jackknifing procedure. The best fitting model was chosen by minimising quasi-Akaike Information Criterion value (qAIC). For a more detailed description of the models see Whitehead (1995). Formulation and parameters of the models are given in Appendix 2.

Model of association Parameter	Value	(SE range)
All animals		
Casual acquaintances		
Number of casual associates	4.5	(4.2–4.8)
Duration of casual acquaintance	5.3 years	(2.9–31.9)
Yearling/subadult – adult		
Constant companions + Casual acquaintances		
Number of casual associates	1.7	–
Duration of casual acquaintance	40.3 days	(19.0–328.1)
Number of constant companions	1.4	–
Yearlings/subadults		
Casual acquaintances		
Number of casual associates	3.6	(3.5–3.7)
Duration of casual acquaintance	10.74 years	(4.4–25.2)

## 4.7. Social network

### 4.7.1. Network structure, genetic relatedness and spatial relationships

Analysis of social network structure was performed on two separate networks constructed using association data from years 2008 and 2009 (Figs 9a and 9c). Clustering of modularity matrix divided the networks into 6 and 8 clusters (hereafter social units), respectively (Figs 9a,c). Modularity was maximised at 0.684 (2008) and 0.764 (2009) indicating strong division and marked structuring of the networks (values >0.3 indicate good division, Newman and Girvan 2004). The average size of social unit was  $4.5 \pm 1.8$  (mean  $\pm$  SD) individuals. However, correcting social unit size for mark rate (61%) resulted in the expected social unit size of 7 individuals. Social units generally corresponded to the family groups determined from capture data (Figs 9a,c). On three occasions, two family groups were merged to form social units (green symbols in 2008 and dark grey in 2009, Fig. 9), and 6 individuals not associated in the family groups (i.e. solitary) were assigned to social units.

Both in 2008 and 2009, the degree of relatedness was higher among individuals within social units than between them. Intra-unit level of relatedness was, however, less than half of the value observed within family groups (Table 11). Since similar patterns were observed in both years of the study, the data were pooled for sex-specific analysis to increase its power. Adult females sharing membership of the social unit were more related among themselves than those belonging to different units and, similarly to the overall pattern, the degree of relatedness within social units was less than half of that observed within family groups (Table 12). Contrastingly, the degree of relatedness between adult females and adult males within and among social units did not differ (Table 12). The only two adult male – adult male dyads that were identified within social units (ID 2 – ID 35 and ID 26 – ID 41, Figs 9a and 9c, respectively) consisted of unrelated individuals (relatedness coefficient -0.06 and -0.17).

Overall, the overlap of space utilisation distribution was significantly higher among individuals within social units than between them (Table 11). The same pattern held true if only adult females and adult female – adult male dyads were considered (Table 12). Additionally, spatial overlap within social units (mean  $\pm$  SE;  $0.583 \pm 0.022$ ) was markedly higher compared to the average overlap observed among all studied animals irrespectively of the social unit membership ( $0.154 \pm 0.008$ ). Spatial overlap was positively correlated with association strength (HWI) (Mantel test:  $r = 0.81$ ,  $n = 900$ ,  $P < 0.001$ , 10 000 permutations). These results indicate that spatial proximity and spatial interactions were largely reflected in social structure. Genetic relatedness showed an evident sex-specific effect on the strength of social bond (Table 8) and social unit membership (Table 12).

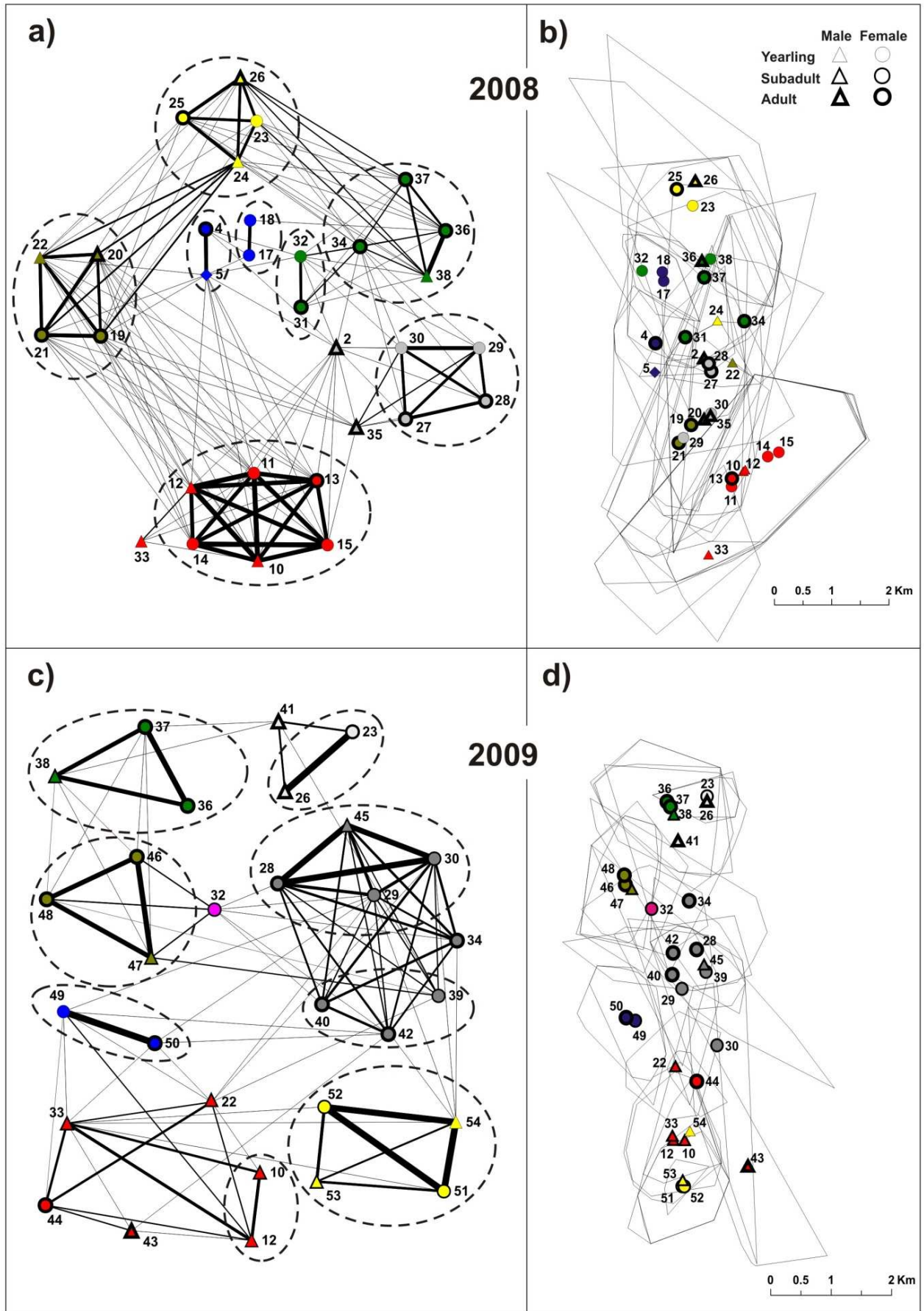


Fig. 9. – For explanation see p. 46

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Explanation to Fig. 9 (p. 45)

Fig. 9 a), c). The social network of wild boar based on associations data from year 2008 (a) and 2009 (c). Nodes and numbers symbolise individual animals, lines represent social ties. The thickness of the line corresponds to the strength of social bond. Network structure was determined using modularity matrix clustering, and membership of social units resulting from the analysis is colour-coded. Network structure is solely derived from social interaction data. Broken-line encircles individuals that had been captured together and remained closely associated for at least 2 months afterwards (family groups). b), d). Spatial distribution of the individuals within the study area in 2008 (b) and 2009 (d). Location of the individual's symbol corresponds to its home range centroid and colours of the symbol indicates social unit membership. Polygons represent area of 90% MCP home range.

Table 11. Mean ( $\pm$  SE) relatedness and spatial overlap between individuals in the wild boar social network in years 2008-2009. Average relatedness and spatial overlap are given for individuals sharing membership of the family group or social unit (within) and those associated with different groups or units (between). Family groups refer to animals trapped together which remained closely associated afterwards, whereas social units result from network partitioning based solely on associations frequency (see Fig. 9). Statistical significance of the differences was obtained with randomisation tests based on 10 000 permutations.

Year Parameter	Family groups			Social units		
	within	between	P	within	between	P
2008						
Relatedness	0.301 $\pm$ 0.030	-0.014 $\pm$ 0.008	<0.001	0.158 $\pm$ 0.030	-0.013 $\pm$ 0.009	<0.001
Spatial overlap	0.768 $\pm$ 0.023	0.110 $\pm$ 0.006	<0.001	0.581 $\pm$ 0.035	0.098 $\pm$ 0.006	<0.001
2009						
Relatedness	0.224 $\pm$ 0.040	0.000 $\pm$ 0.010	<0.001	0.078 $\pm$ 0.028	0.001 $\pm$ 0.010	0.004
Spatial overlap	0.670 $\pm$ 0.053	0.101 $\pm$ 0.008	<0.001	0.584 $\pm$ 0.030	0.065 $\pm$ 0.006	<0.001
All						
Relatedness	0.277 $\pm$ 0.026	-0.008 $\pm$ 0.006	<0.001	0.122 $\pm$ 0.022	-0.007 $\pm$ 0.007	<0.001
Spatial overlap	0.730 $\pm$ 0.025	0.106 $\pm$ 0.005	<0.001	0.583 $\pm$ 0.022	0.082 $\pm$ 0.004	<0.001



Table 12. Mean ( $\pm$  SE) relatedness and spatial overlap among all wild boar, among adult females, and between adult females and adult males in the social network in years 2008-2009. Average relatedness and spatial overlap are given for individuals sharing membership of the family group or social unit (within) and those associated with different groups or units (between). Statistical significance of the differences was obtained with randomisation tests based on 10 000 permutations.

Parameter	Family groups			Social units		
	within	between	P	within	between	P
Relatedness						
All animals	0.277 $\pm$ 0.026	-0.008 $\pm$ 0.006	<0.001	0.122 $\pm$ 0.022	-0.007 $\pm$ 0.007	<0.001
Ad. F - ad. F	0.259 $\pm$ 0.069	-0.021 $\pm$ 0.020	<0.001	0.116 $\pm$ 0.070	-0.020 $\pm$ 0.020	0.008
Ad. F - ad. M	-	-	-	0.085 $\pm$ 0.080	-0.025 $\pm$ 0.025	0.068
Spatial overlap						
All animals	0.730 $\pm$ 0.025	0.106 $\pm$ 0.005	<0.001	0.583 $\pm$ 0.022	0.082 $\pm$ 0.004	<0.001
Ad. F - ad. F	0.671 $\pm$ 0.083	0.128 $\pm$ 0.016	<0.001	0.593 $\pm$ 0.058	0.089 $\pm$ 0.012	<0.001
Ad. F - ad. M	-	-	-	0.502 $\pm$ 0.091	0.108 $\pm$ 0.016	<0.001

#### 4.7.2. Variation in sociality

Individual sociality was quantified by three network centrality measures (strength, eigenvector centrality, and clustering coefficient), which describe position and connectivity of an individual within the social network.

The strength of the individual, measuring how strongly an individual associates with the others, averaged  $1.65 \pm 0.15$  (mean  $\pm$  SE). The best model explaining variation in strength included sex, age and the interaction between them (Table 13). Although the overall effect of sex was insignificant (Table 14), changes in strength among age classes varied between sexes, as indicated by significant interaction term (Tables 13 and 14). Yearlings demonstrated the highest strength (Fig. 10a, Table 14) which dropped sharply, when they reached the age of subadults. This effect was significantly more subtle in females. Subadult females, compared to males, tended to increase the strength of their associations with other individuals when reaching adulthood, as indicated by a significant interaction term (Fig. 10a, Table 14).

The second measure, eigenvector centrality, integrates strength of a given individual and its neighbours (associates) and measures how well an individual is connected within the network. The eigenvector centrality averaged  $0.09 (\pm 0.02)$  and its variation was mainly shaped by the age of an individual but each sex exhibited a different pattern of decrease in this measure throughout their lifetime (Fig. 10b, Table 14). Yearlings tended to show the best connectivity within the network (i.e. the highest eigenvector centrality values). Subadult females maintained similar level of this parameter which, in contrast, continued to decline in males until adulthood (Fig. 10b, Table 14).

The third measure, clustering coefficient, is the proportion of an individual's neighbours that are themselves neighbours and thus describes how well associates of the focal individual are interconnected. The mean clustering coefficient was  $0.37 (\pm 0.03)$  and variation of this measure was best explained by the model containing age only (Table 13). Similarly to other centrality measures, the clustering coefficient decreased throughout the life of individuals (Fig. 10), probably as an effect of yearlings becoming less dependent on the group and associating more outside their natal groups.

Thus, social behaviour of an individual appeared to vary according to its age and sex (Fig. 10, Table 13). Overall, age appeared the main factor influencing individual's position and role in the social network. Network cohesion was largely maintained by young animals. Older animals tended to be more peripheral in terms of connectivity with the amplitude of this effect modified by sex.

Table 13. The sets of generalized mixed models analysing effects of sex and age of the individual on three centrality measures (strength, eigenvector centrality, clustering coefficient; see explanation to Fig. 10) calculated for each individual wild boar ( $n = 60$ ) forming social networks in Bialowieża Primeval Forest in 2008-2009. Included in the table are corrected Akaike Information Criterion (AIC<sub>c</sub>) values and the difference between each model and the best fitting model ( $\Delta$ AIC<sub>c</sub>), number of model parameters (k), and the Akaike's weights ( $\omega_i$ ). The models were ranked in ascending order of the AIC<sub>c</sub> values (the most parsimonious models are on the top of each list).

Parameter	Model	k	AIC <sub>c</sub>	$\Delta$ AIC <sub>c</sub>	$\omega_i$
Strength	Age + Sex + Age×Sex	9	394.7	0.00	>0.999
	Age + Sex	7	432.1	37.40	<0.001
	Age	6	432.2	37.48	<0.001
	Null	4	570.4	175.65	<0.001
	Sex	5	571.4	176.70	<0.001
Eigenvector centrality	Age + Sex + Age×Sex	9	191.9	0.00	0.963
	Age + Sex	7	199.7	7.82	0.019
	Age	6	199.9	8.04	0.017
	Null	4	258.8	66.90	<0.001
	Sex	5	260.3	68.39	<0.001
Clustering coefficient	Age	5	304.4	0.00	0.507
	Null	3	306.1	1.75	0.212
	Age + Sex	6	306.6	2.21	0.168
	Sex	4	307.7	3.34	0.096
	Age + Sex + Age×Sex	8	311.0	6.62	0.018

Table 14. Parameters estimated from the generalized mixed effects models included in the most parsimonious model (according to AIC<sub>c</sub>) analysing effects of sex and age of the individual on three centrality measures (strength, eigenvector centrality, clustering coefficient; see explanation to Fig. 10) calculated for each individual wild boar (n = 60) forming social networks in 2008-2009. Sex and age were fitted as factor variables with “male” and “yearling” as reference levels, respectively. The models were fit with error structure following Poisson distribution. Response variables were multiplied by 100 before fitting to achieve integers. SE = standard error, CL = confidence limit. Variables with the 95% CLs of estimates not spanning zero are in bold.

Parameter	Estimate	SE	95% lower CL	95% upper CL	P
Strength					
<b>Intercept</b>	4.943	0.247	4.459	5.427	<0.001
<b>Age (subad. vs. yearling)</b>	-1.055	0.077	-1.205	-0.904	<0.001
<b>Age (ad vs. yearling)</b>	-0.525	0.188	-0.894	-0.155	0.005
<b>Sex×Age (female×subad.)</b>	0.630	0.095	0.443	0.817	<0.001
Sex×Age (female×adult)	0.343	0.212	-0.073	0.758	0.106
Sex (female vs. male)	-0.155	0.118	-0.387	0.076	0.188
Random effects	Variance	SD			
Individual ID	0.048	0.219			
Group ID	0.731	0.855			
Network ID	0.031	0.175			
Eigenvector centrality					
Intercept	0.769	1.139	-1.463	3.002	0.499
<b>Age (subad. vs. yearling)</b>	-5.069	0.675	-6.392	-3.747	<0.001
<b>Age (ad vs. yearling)</b>	-2.713	1.273	-5.208	-0.218	0.033
<b>Sex×Age (female×subad.)</b>	3.973	1.089	1.838	6.108	<0.001
Sex×Age (female×adult)	2.187	1.502	-0.757	5.131	0.145
Sex (female vs. male)	-1.091	0.912	-2.878	0.696	0.231
Random effects	Variance	SD			
Individual ID	1.558	1.248			
Group ID	6.939	2.634			
Network ID	0.999	0.999			

Table 14. – continued on the next page

Table 14. – concluded.

Parameter	Estimate	SE	95% lower CL	95% upper CL	P
Clustering coefficient					
<b>Intercept</b>	2.943	0.297	2.360	3.525	<0.001
<b>Age (subad. vs. yearling)</b>	-0.187	0.076	-0.336	-0.037	0.014
Age (ad vs. yearling)	-0.039	0.087	-0.209	0.131	0.653
Random effects	Variance	SD			
Individual ID	0.019	0.138			
Group ID	1.608	1.268			

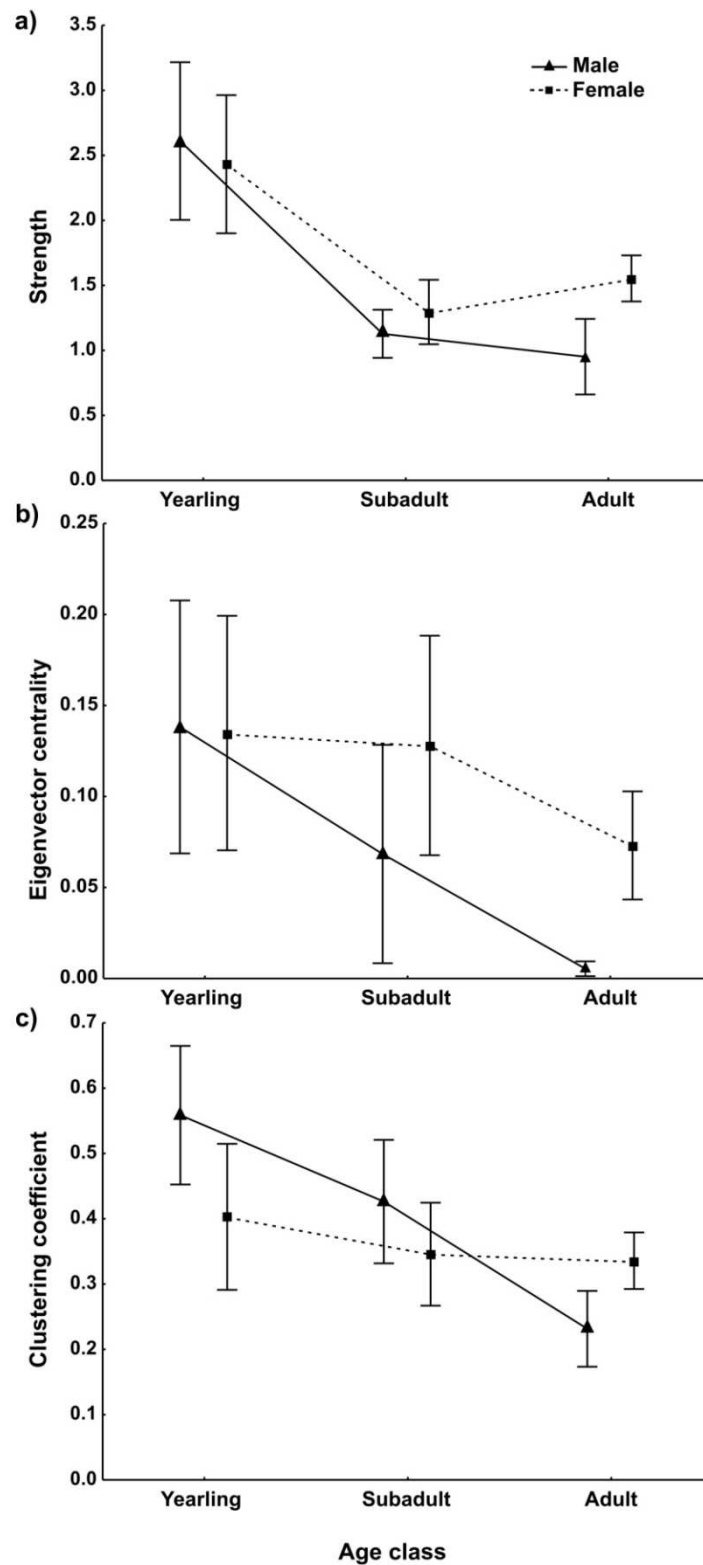
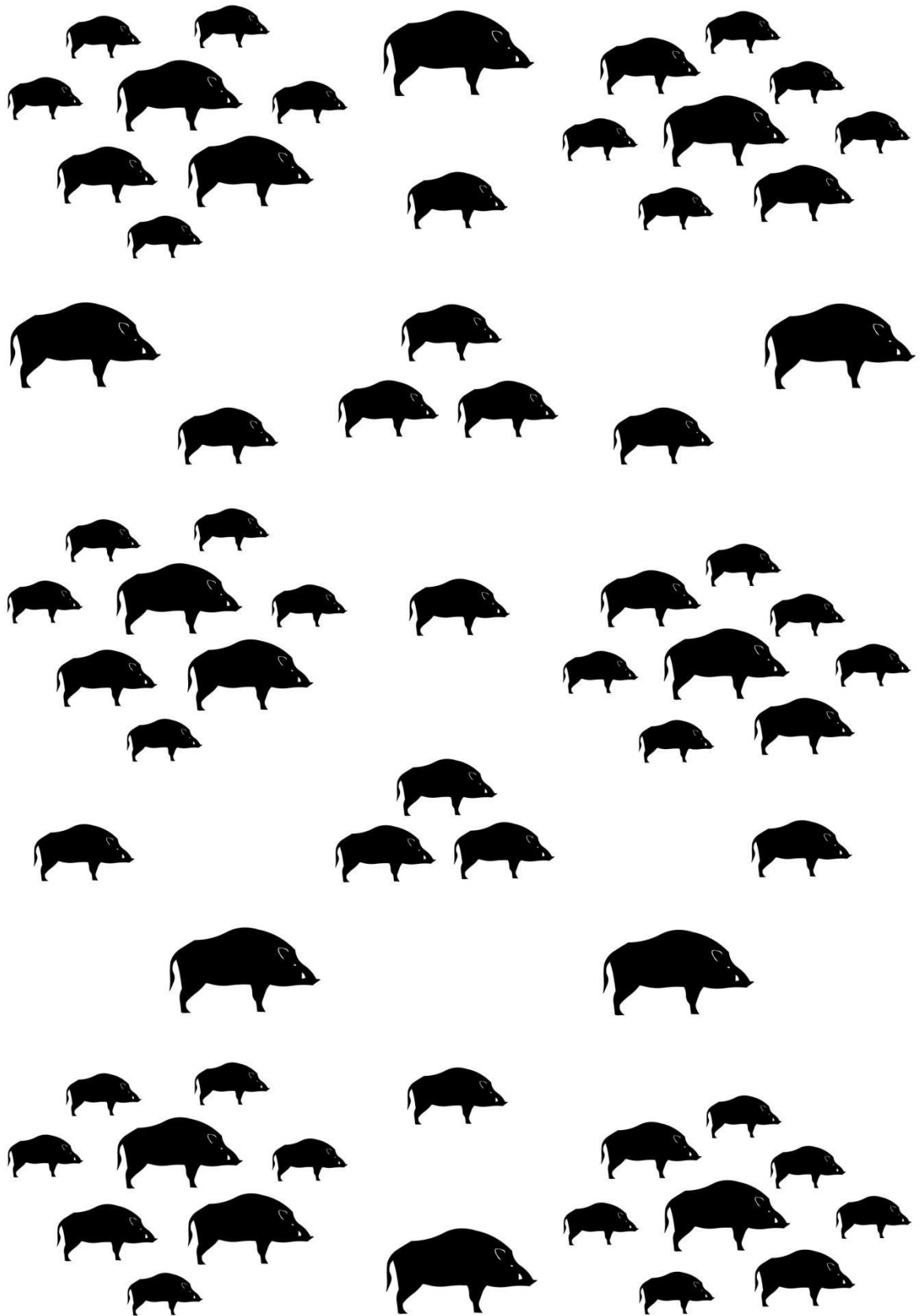


Fig. 10. Observed values of the three centrality measures which describe position and connectivity of an individual within the social network: a) Strength - measures how strongly an individual associates with the others, b) Eigenvector centrality - how well an individual is connected within the network, c) Clustering coefficient - how well associates of the focal individual are interconnected; calculated for individual wild boar ( $n = 60$ ) forming social networks in 2008-2009.



## 5. DISCUSSION

### 5.1. Recapitulation of the results

Associations and network analysis has been increasingly used over the last years to study social interactions and structural properties of social organisation across variety of taxa: from social insects (Fewell 2003, Naug 2008), over fish (Croft et al. 2005), reptiles (Godfrey et al. 2009), birds (McDonald 2007), to cetaceans (Lusseau et al. 2006, Wiszniewski et al. 2010), and primates (Flack et al. 2006, Henzi et al. 2009). Network approaches provide powerful ways to comprehensively analyse relationships between social and genetic structure in wild populations, yet such studies are rare. Only few studies combined explicitly network-based analysis of social structure with genetic data to investigate a link between genetic relatedness and association patterns (bottlenose dolphins *Tursiops sp.*: Wiszniewski et al. 2010, Galapagos sea lions: Wolf and Trillmich 2008, long-tailed manakins *Chiroxiphia linearis*: McDonald 2009, guppies *Poecilia reticulata*: Croft et al. 2012). To my knowledge, this study is the first one in terrestrial vertebrate to combine telemetry-derived data on associations, network analytical tools, and genetic information to explore the link between kinship and social behaviour.

Recording dyadic spatial proximity (associations) approximates situations in which actual interactions might occur. Previous studies inferred association patterns from direct observations of identifiable individuals what ensured that associating individuals were in direct contact. This study utilises mainly indirect, radio-tracking records of associations. Therefore, it could be a source of bias, because the approach requires setting spatial proximity threshold between associating individuals to take into account radio-tracking error. The threshold used here (up to 350 m) was conservative, i.e. included a maximum of 60% of associations which would have been recorded, if the mere radio-tracking error of 153 meters was used. I also believe that the threshold used allowed communication via olfactory and auditory cues which are the most commonly used in intraspecific interactions of wild boar. Generally, the coherence of the results obtained with trapping, genetic and association data indicates that meaningful associations were recorded. The problem did not occur when GPS locations were used due to their high spatial accuracy.

The wild boar population in the Białowieża National Park is largely driven by natural processes. Long-term dynamics of population numbers is mainly shaped by winter severity, which increases natural mortality, and by cyclic masting of trees, which enhances reproduction and survival. Mortality is primarily caused by diseases and starvation, followed by wolf predation. Hunting and logging is not allowed within the BPF. Moreover, forest



composition is characterised by high share of natural stands and old-growths which harbour rich community of ungulates and large predators. Therefore, the results of this study describe patterns in wild boar population as natural as possible in contemporary temperate woodlands of Europe.

The average family group size estimated from the trapping data, as well as from analyses based on social interactions alone, was seven individuals. The vast majority of adult females and young animals (<2 years old) were associated in groups, whereas adult males were mostly solitary. Individuals associated in groups were significantly more genetically related to each other than solitary individuals. On average, the intra-group level of relatedness corresponded to second-degree relatives. Within a group relatedness was negatively correlated with group size. Members of the family groups showed extensive spatial overlap, whereas little space was shared by animals from different family groups. Ranging patterns were uniform across sexes but varied with age, with subadults occupying the smallest home ranges.

Wild boar formed non-random, preferential, stable and long-lasting associations. The temporal stability of associations was particularly strong among adult females and animals forming family groups. Conversely, adult males formed short-lived associations disintegrating within a few days. The frequency of fission-fusion events (be it of single individuals or groups) was moderately low. There was a strong correlation between association strength and genetic relatedness but kin-targeted interactions extending beyond spatial proximity were observed only among females.

On the population level, there was a negative relationship between geographic distance and genetic relatedness. Genetic structure was detected only at a small spatial scale (up to 5 km) which corresponds to the size of 2-3 home ranges in the studied population. Genetic structure was maintained at the same distance in males and females. However, females showed a stronger relationship between genetic and spatial distance at short distances (0-1 km) while males showed stronger structuring in the second distance class (1-5 km). Based on population genetics, I found little evidence for sex-biased dispersal, yet there was a tendency towards greater dispersal in males. Telemetry data on dispersal provided results consistent with genetic data: the majority of young wild boar of both sexes remained within or in close vicinity of the maternal home range. Males tended to disperse further away from the natal area than females while frequency of dispersal was not sexually biased. Dispersal occurred at the age of 18-21 months.

The social network, derived solely from association data, was spatially structured with well defined and cohesive social units. The close match of the social structure revealed in

social units and family groups (obtained from trapping and genetic data) indicated that they mirror the same level of social organisation. Space utilised by the members of a given social unit overlapped extensively while little overlap was observed across social units. However, spatial distribution and overlap of individuals could not entirely explain the association patterns and network structure. Association and genetic data indicated that active social preferences and targeted interactions played important roles in shaping the social structure of the population. Wild boar within the same social units, alike family groups, were more related to each other than to members of other social units. High intra-unit relatedness among adult females supports matrilineal nature of the social units. Conversely, adult males and adult females associated in the same social units were not related.

Sociality of wild boar generally decreased with age of the individuals, and the magnitude of the effect was modified by sex. Young wild boars showed the strongest and most diverse connections within the network. The onset of dispersal marked a decrease in sociality, which was manifested stronger in males than females. Similarly, grouping tendency was the highest among yearlings and decreased with age, mildly in females and sharply in males. These results highlight the role of young wild boar in maintaining the cohesion of the social network.

Given the natural environmental setting of the study population and its virtually undisturbed character and history (limited hunting, no translocations), I believe that observed patterns and processes of social relationships represent reference picture of the social structure of wild boar inhabiting lowland forests of European temperate zone.

## **5.2. Grouping patterns - demography, relatedness, and spatial relationships**

Overall, behavioural and genetic data showed high sociability and confirmed matrilineal composition of family groups within the study population. Trapping data showed that average group comprised seven individuals. Interestingly, similar estimate was obtained based on social interactions alone. Analysis of temporal patterns of associations and network structure resulted in a group size of 8 and 7, respectively. A group was typically composed of 1-2 adult females, several yearlings, and a few subadults. In a sample of captured wild boars, the vast majority of adult females and young individuals (< 2 years old) was associated in groups, whereas most of adult males were solitary. Group size in wild boar show high variation and ranges from 2 to 28 individuals (wild boar: Rosell et al. 2004, Poteaux et al. 2009; free-ranging feral pigs: Gabor et al. 1999). In the BPF, Lebedeva (1956) reported group size of 3-5 individuals in the period of low population density (years 1946-1953), whereas Jędrzejewska and Jędrzejewski (1998) documented an average group size of 4-6 in years of

moderate and high density (1986-1995). Average group size found in the present study is similar to estimates found across variety of geographical locations: 7 inds in north-eastern France (Poteaux et al. 2009), 4 inds in northern Spain (Rosell et al. 2004), and 6 inds in Texas, USA (Gabor et al. 1999).

In wild boar, extended postweaning associations between mother and offspring lead to the formation and persistence of matrilineal structures (Kaminski et al. 2005). This process has been shown to drive the emergence of kin structures in several mammalian species, e.g. yellow-bellied marmots *Marmota flaviventris* (Armitage 1998) and ringtailed lemurs *Lemur catta* (Nuun and Pereira 2000). In the present study, wild boar group composition was largely shaped by kinship, i.e. relatedness among individuals within groups were significantly higher than across groups and among solitary individuals. On average, the intra-group level of relatedness corresponded to second-degree relatives but a wide distribution of pairwise relatedness values indicated the presence of both unrelated and fully related individuals in the groups. In fact, however, all analysed groups but one contained fully related individuals, be it mother with offspring or full siblings, which made up 80% of the group members. Therefore, despite observed deviation from the full relatedness hypothesis, observed groups appeared to be matrilineal, family groups. This finding is consistent with previous studies on wild boar (Kaminski et al. 2005, eastern France; Poteaux et al. 2009, north-eastern France; but see Iacolina et al. 2009 for non-kin associations in Tuscany, Italy). However, the level of intra-group relatedness found in the present study was higher than previously reported for wild boar in central Italy (Iacolina et al. 2009), north-eastern France (Poteaux et al. 2009) and feral pigs in Australia (Spencer et al. 2005). This seem to confirm the previously suggested disturbing effect of hunting on wild boar social structure as it shows higher stability of kin-based associations in the absence of hunting.

The wide distribution of pairwise relatedness coefficient among yearlings and between adult females and yearlings in the studied population indicated that multiple litters of different females were associated in family groups. This was supported by an inverse relationship between intra-group relatedness and group size. On the other hand, exceptionally high level of relatedness among subadults and adult females within family groups (0.37 and 0.38, respectively) suggests that recruitment into existing matrilineal structures or formation of new ones involved highly related individuals (i.e. first- or second-degree relatives). This is in accordance with the findings of Kaminski et al. (2005) from eastern France showing that yearling females from one social group tended to leave or stay in the natal group collectively.

Kin structures, such as wild boar matrilineal groups, enhance the benefits of group living by increasing the indirect component of inclusive fitness. This is achieved by kin-directed social learning and cooperative behaviours and includes acquisition of information about resources (e.g. food patches, breeding and refuge sites), predation avoidance strategies, cooperative foraging and breeding (West et al. 2002, 2007, White and Cameron 2009, Williams et al. 2013). Helping behaviours, such as assistance in thermoregulation, anti-predatory vigilance and defence, can be particularly advantageous strategy to optimise foraging and rearing of young when multiple litters are present simultaneously in a group. This strategy is likely to be represented in wild boar, the species that exhibits high synchrony of reproduction within one social group (Delcroix et al. 1990) and produces large litters (Carranza 1996, Servanty et al. 2007). Alloparental care is particularly rewarding and should be promoted in matrilines, where the gain in fitness benefits is increased as a result of helping relatives (but see Clutton-Brock 2002 for the review). Winter severity has been shown to be a main factor affecting the survival and reproduction of wild boar (Jędrzejewska and Jędrzejewski 1998, BPF, Poland; Geisser and Reyer 2005, north-eastern Switzerland). Therefore, achieving good body condition and gaining sufficient fat reserves before winter is crucial for wild boar fitness. In the BPF, the acorn crop occurring in autumn is the most efficient way to achieve the above (Jędrzejewska and Jędrzejewski 1998). Individual oaks show high variation in acorn production (Koenig et al. 1990, Healy et al. 1999, Greenberg 2000, T. Podgórski, unpublished data), creating heterogeneous distribution of food resources in this crucial period. Therefore, acquiring information on high quality food patches would be advantageous to young animals and would encourage philopatry. It has been shown that foraging efficiency can be considerably improved by information obtained through social learning (Laland and Plotkin 1990, Midford et al. 2000, Galef and Laland 2005) and use of spatial memory (Edwards et al. 1996). Nevertheless, beneficial effects and adaptive value of kin structures in wild boar populations have not yet been evaluated and need further investigation.

In the present study, members of the family groups showed extensive spatial overlap, whereas little space was shared by animals from different family groups. This is indicative of significant group effect on space use patterns, strong site fidelity, and, consequently, potential for cooperative behaviours (e.g. foraging). Strong spatial segregation was paired with distinct genetic structuring, i.e. individuals within family groups were more related to each other than across groups. This positive relationship between spatial and genetic structure corresponds to the idea that kin structure can arise from limited dispersal alone and does not necessarily

imply any targeted, beneficial interactions among kin. Indeed, studies have demonstrated that genetic structure can emerge as by-product of philopatry through a passive process of accumulating relatedness locally (Fowler 2005, Campbell et al. 2008). However, spatial segregation might not entirely explain the observed kin-based structure as targeted interactions among kin can occur within spatially structured populations (Wolf and Trillmich 2008). Indeed, fine-scale analysis of association preferences in the studied wild boar population showed that spatial segregation does not fully account for the observed grouping patterns.

Wild boar exhibit remarkable intraspecific variation in home range size (see Keuling et al. 2008 for review). Some studies reported larger home ranges in male wild boar in Italy (Morini et al. 1995) or feral pigs in California, USA (Baber and Coblenz 1986) and Australia (Saunders and Kay 1991), whereas no sex-related differences were found in other Italian wild boar populations (Boitani et al. 1994, Massei et al. 1997) and north-American populations of feral pigs (Wood and Brenneman 1980, Singer et al. 1981). Home range size in females did not vary with age (Keuling et al. 2008). Generally, wild boar shows considerable spatial behavioural plasticity across a wide range of geographic locations and habitats (Spitz 1992, France; Boitani et al. 1994, Italy; Massei et al. 1997, Italy; Podgórski et al. 2013, Poland). In the present study, home range size (90% MCP) averaged 3.3 km<sup>2</sup>, which was an intermediate value compared to other studies. Ranging patterns appeared to be uniform across sexes as similar-sized home ranges were occupied by both sexes in each age class. Space use patterns varied with age: while home ranges of yearlings and adults were comparable in size, subadults had significantly smaller home ranges compared to other age classes. In fact, subadults occupied an area roughly one-third the size of that in other age classes. This pattern was consistent across sexes. In this study, home range estimates were built upon 90% of locations and thus represented permanently used areas. In southern France, Cousse et al. (1994) showed that young wild boar tended to move temporarily out of the natal area. Possibly, those pre-dispersal exploratory movements could not be fully recorded in the present study due to the limitations of radio-tracking, thus leading to underestimation of subadults' home ranges.

### **5.3. Spatial genetic structure of the population – effect of limited dispersal**

Social organisation is largely shaped by population genetic variation and structure which can determine, for example, patterns of associations (Dobson et al. 1998). At the same time, social relationships (grouping patterns, mating strategies, dispersal) influence the genetic make-up of the population (Sugg et al. 1996, Storz 1999, Krützen et al. 2003). In the present study, I evaluated the spatial genetic structure of the wild boar population to make

inferences on its social organisation. The analysis highlighted how dispersal operates on an individual and population level.

Overall, there was a slight yet significant negative relationship between geographic distance and genetic relatedness indicating the presence of local kin clusters and the importance of philopatry in shaping the structure of wild boar population. This was supported by the results of the spatial autocorrelation analysis. Genetic structure was detected only at a small spatial scale corresponding to the size of few home ranges in the study population. It means that for the majority of individuals, their nearest neighbour was their close relative. The non-random genetic structure observed only over short distances is usually associated with limited dispersal (Peakall et al. 2003, Coster and Kovach 2012). Given that my analysis concerned only adult animals and thus reflected post-dispersal situation, the observed spatial genetic structure is indicative of reduced natal dispersal. Interestingly, a similar spatial genetic structure was observed in males and females inferring comparable gene flow in both sexes and lack of sex-biased dispersal. However, fine-scale differences in the strength of the spatial genetic correlation between sexes suggested that males and females may differ in dispersal strategies at small spatial scales (<5 km). The relationship between genetic and spatial distance was significantly stronger in females at short distances (0-1 km), while males showed stronger structuring in the distance class of 1-5 km. This may reflect females' tendency to settle in a direct neighbourhood of a kin. Similarly to genetic structure analysis, assignment index also provided little evidence for sex-biased dispersal. No significant differences between sexes in dispersal frequency were found using assignment index ( $AI_c$ ) and its variance. Despite the statistical insignificance, however, both estimates indicated a tendency towards somewhat greater dispersal in males than in females.

Previous studies have supported male-biased dispersal in wild boar. Poteaux et al. (2009) found spatial genetic structure in females but not in males. Mark-recapture data also revealed a male bias both in dispersal frequency (Keuling et al. 2010, northern Germany) and distance (Truvé and Lemel 2003, southern Sweden). These findings are consistent with the dominant type of natal dispersal in mammals, particularly in group-living species with polygynous mating system (Greenwood 1980, Dobson 1982, Smale et al. 1997). However, a number of species across various mammalian taxa lack sex-biased dispersal, e.g. Canada lynx *Lynx canadensis* (Campbell and Strobeck 2006), kangaroo rat *Dipodomys spectabilis* (Edelman 2011), fat-tailed dwarf lemur *Cheirogaleus medius* (Fredsted et al. 2007), snowshoe hare *Lepus americanus* (Burton and Krebs 2003). No bias is expected when socio-ecological factors (e.g. competition for resources or mates) equally affect the reproductive success and

survival of males and females (Smale et al. 1997, Perrin and Mazalov 2000). Thus, lack of sex-biased dispersal is common in monogamous and solitary species of mammals (Greenwood 1980, Dobson 1982, Smale et al. 1997). For example, solitary kangaroo rats defend territories surrounding complex burrow systems. Ownership of these burrows is crucial for the survival of both males and females and thus promotes equal dispersal of both sexes (Edelman 2011). In polygynous species, lack of sex bias is expected if competition for resources limits the reproductive success of females, whereas male bias should occur when competition for mates is prevailing, i.e. resources do not limit female fitness (Perrin and Mazalov 2000). In the study population, proportion of males among adults was 33% suggesting low competition for mates among males which could be a reason for insignificant sex-bias in dispersal. However, effect of resources availability on females reproductive success remains unknown and needs further investigations.

The analysis of dispersal variation of the individually radio-marked yearling wild boar provided results consistent with genetic data. The majority of individuals remained within or in close vicinity of maternal range. Males tended to disperse further away from the natal area while frequency of dispersal was not sexually biased. Consequently, such dispersal patterns were reflected in the spatial genetic structure of adult animals. Secondary dispersal observed in adult wild boars was incidental and could not affect population genetic structure. Previous studies from southern Sweden (Truvé and Lemel 2003) and northern Germany (Keuling et al. 2010) found dispersal to be highly skewed towards short distances (few kilometres) with males covering longer distances. These findings are consistent with my results and suggest a limited spatial extent of wild boar dispersal, i.e. majority of young wild boars remain within or in close vicinity of their natal home ranges. In contrast to the result of Poteaux et al. (2009) and Keuling et al. (2010), I found no evidence supporting more frequent dispersal in males. Timing of dispersal observed in the present study corresponds to previously reported age of >16 months (Gabor et al. 1999, Keuling et al. 2010). Naturally, disappearance of young wild boar from the population is not only due to dispersal but also, and even to greater degree, due to mortality. In the BPF, Lebedeva (1956) estimated mortality of piglets in their first year of life at 40% of the animals born. In the Kampinos National Park, Poland, Jezierski (1977) estimated natural mortality of wild boar at 48% and 36% in the first and second year of life, respectively.

Dispersal has evolved as a strategy to circumvent negative effects of inbreeding and kin competition (Gandon and Michalakis 2001) with male-biased dispersal dominating in mammals (Greenwood 1980, Dobson 1982). Sexual bias in wild boar dispersal was weakly

manifested in the present study, which is intriguing in a species with a polygynous mating system. It is likely, however, that observed fine-scale differences in dispersal distances provide a sufficient level of spatial segregation to avoid mating and competing with relatives. Other mechanisms, such as female preferences for mating partners, may additionally prevent breeding with related males (Höner et al. 2007). For example, in pilot whales *Globicephala spp.*, both females and males commonly remain in the natal groups but females typically mate with members of other social groups (Amos et al. 1993).

#### **5.4. Genetic and temporal effects on association patterns**

##### ***5.4.1. Effect of relatedness on association patterns***

Generally, wild boar in the study population formed non-random, preferential associations. The pattern was observed in both analysed years suggesting its temporal stability. The majority of dyads did not associate, most probably due to spatial segregation. On the other hand, some pairs of individuals formed strong associations, spending over half of their time together. Although studies allowing comparison with other wild boar populations are lacking, such association patterns are expected for group-living animals and have been reported for other social species such as Galapagos sea lions (Wolf et al. 2007), bottlenose dolphins (Lusseau et al. 2006, Wiszniewski et al. 2010), and guppies (Croft et al. 2005).

I found no sexual segregation in terms of social connectivity in the studied wild boar population. Both males and females associated indifferently, however, the temporal nature of the interactions differed significantly between sexes. Intersexual social ties have been shown to play an important role in maintaining the cohesion of the social network in bottlenose dolphin populations and were attributed to reproductive strategies and environment heterogeneity (Lusseau et al. 2003, Wiszniewski et al. 2010). In wild boar populations, sexual segregation has not been systematically investigated yet. Body size dimorphism, which diversifies energy demands, foraging and anti-predatory strategies and thus leads to separation of sexes in space and time, is generally responsible for sexual segregation in ungulates (Ruckstuhl and Neuhaus 2002). Ecological segregation (in diet and habitat use) of sexes correlates positively with body size dimorphism between sexes in browsers but not in non-ruminants, such as wild boar (Myrsterud 2000). In wild boar, sexual dimorphism in body size is not apparent through juvenescence and adolescence, reaching a moderate value of approximately 20% in adult animals (Moretti 1995, Pedone et al. 1995). This difference, paired with sex-specific life histories, might be important in predation risk management and can, among other factors, contribute to sex separation in adults only. In the conditions of BPF,



wild boar is predated by wolf (19% of annual natural mortality) and very rarely by lynx (1%) (Jędrzejewska and Jędrzejewski 1998). Wolf impact is heaviest on the youngest cohorts: juveniles and yearlings (70% of wild boar killed by wolves) (Jędrzejewski et al. 2000). Therefore, grouping as a strategy to minimise predation risk is beneficial for adult females with offspring and young animals but not for adult males which can defend themselves and are rarely attacked (Kudatkin 1982, Jędrzejewski et al. 1992, 2000, Quenette and Gerard 1992)

The strong correlation between association strength and genetic relatedness indicates that wild boars in BPF spend more time with individuals to which they are more related. This could have been an effect of mere spatial distribution of individuals, i.e. animals closer to each other having greater chance of interacting with kin neighbours due to cross-generational site fidelity. However, the positive relationship between strength of social bond and relatedness held true when spatial proximity was accounted for, indicating the presence of targeted interactions among kin. Behavioural mechanisms and benefits of these associations in wild boar are not well understood. It is not possible at this point to determine foraging or reproductive advantages of preferential kin associations. If inclusive fitness benefits are the main drivers of targeted kin interactions in matrilineal system, we should expect interactions among related females to be favoured in wild boar. Indeed, the data showed that females associated preferentially with related females, even when spatial proximity was accounted for. This result provides ultimate evidence that kin-targeted interactions among females underlie the observed kin structures, which are thus not entirely a result of simplistic, passive process of local accumulation of relatedness. Potentially, direct and indirect fitness benefits of these associations may include increased foraging efficiency, gaining information on resource distribution, anti-predatory defence, increased survival of piglets through cooperative breeding. Social bonds between related females have been demonstrated to have a positive effect on female fitness in other group-living species (e.g. yellow-bellied marmots: Armitage and Schwartz 2000; review in Silk 2007). For example, presence of matrilineal was associated with increased juvenile survival in Townsend's voles *Microtus townsendii* (Lambin and Yoccoz 1998) and lions *Panthera leo* (Packer and Pusey 1995). Furthermore, individual preferences to associate with kin can increase social cohesion at the population level (African elephants: Archie et al. 2006; yellow-bellied marmots: Wey and Blumstein 2010). In contrast to female–female associations in the present study, wild boar males formed associations with unrelated males. Wild boar males compete against each other for access to receptive females and may obtain greater reproductive benefits by reducing competition with related males.

#### 5.4.2. Temporal stability of associations

Overall, the social organisation of the wild boar population in BPF was characterised by stable, long-lasting associations of individuals implying a strong group cohesion. The stability in the dynamics of associations was particularly strong among adult females and animals forming family groups (yearlings, subadults, adult females). Adult males were mainly engaged in dynamic, short-lived associations. Frequency of fission-fusion events (be it of single individuals or groups) was moderately low.

The proportion of casual acquaintances in the population was relatively low indicating moderate fission-fusion dynamics between groups. Short-time, casual relationships among animals forming groups (yearlings, subadults, adult females) ranged from 10 to 17% of all associations and lasted 7-40 days on average. The higher frequency and longer duration of casual acquaintances found in yearlings and subadults may suggest that these cohorts mainly contributed to temporal dynamics of inter-group interactions. This would be consistent with the high connectivity of young wild boars within the social network. Fission-fusion events have been reported from other wild boar populations (Poteaux et al. 2009, north-eastern France) and free-ranging feral pigs (Gabor et al. 1999, Texas, USA) although temporal and demographic effects were not quantified. This study approximates the duration and limited frequency of temporal associations but I could not determine the nature of these associations, i.e. whether they represented temporal associations of permanent social units, transient individuals joining different groups temporarily, or short-time preferred relationships between individuals. Flexible, fission-fusion social organisation, where group composition changes over multiple temporal scales, was found in some highly social species, e.g. bottlenose dolphins (Connor et al. 2000), spotted hyenas *Crocuta crocuta* (Holekamp et al. 1997), African elephants (Wittemyer et al. 2005), and a number of primate species (Aureli et al. 2008). This flexibility may allow individuals to optimise the costs and benefits of group-living according to changes of socio-ecological factors such as availability and distribution of resources, predation pressure, and social interactions (Wrangham 1982, Dunbar 1992, Schaik 1999).

Associations among adult females were stable and long-lasting (potentially life-time long). Only 10% of associations were short-time, yet preferential, acquaintances. At least two, mutually non-exclusive, reasons can underlie this pattern. Long-lasting associations provide time-lag necessary for individuals to develop behavioural reciprocity and to profit from cooperative behaviours. Secondly, philopatry and indirect fitness benefits resulting from matrilineal structure may enhance the stability of social bonds. High levels of intra-group

relatedness (particularly among subadult and adult females) provide more evidence for the temporal stability of kin-based social groups. High temporal stability of relationships between adult females and younger cohorts suggests a high cohesion of social groups and strong clustering of the population. This prediction was confirmed by social network analysis. Interestingly, associations among yearlings in the study population were exceptionally stable and long-lasting, which seems to correspond to the behaviour of collective dispersal or philopatry described by Kaminski et al. (2005) for wild boar in eastern France.

Associations of adult males (with other adult males and females) in this study were short-lived. The majority (65-75%) of male's associations disintegrated within a day and the rest lasted a few days at most. This is consistent with the solitary lifestyle of adult male boars described previously (Dardaillon 1988, Boitani et al. 1994, Gabor et al. 1999). Short-time casual acquaintances, in which adult males engage, may be due to interactions with mating competitors (associations with other males), assessment of females reproductive status (with females), or enhancement of foraging efficiency by utilising social cues provided by groups (with females and/or groups).

## **5.5. Wild boar social network**

### ***5.5.1. Network structure and genetic relatedness***

This study demonstrated non-random and temporally stable patterns of associations in the wild boar population from BPF and revealed social structure that emerged from social association data alone. Hence, structural units resulting from social network analysis are referred to as social units. In both analysed years, wild boar formed well defined, spatially structured, and cohesive social units. Interestingly, the population structure revealed in the social units closely matched the one of family groups (determined from trapping and genetic data), which was reflected in similar group size and composition. On three occasions, however, two family groups (38% of all marked groups) were merged to form social units suggesting frequent interactions between members of those family groups. An individual's membership of the social unit was stable across the two years with only one adult female (ID 34) switching the unit. These results again demonstrate moderate fission-fusion dynamics in the studied population, which is consistent with the analysis of temporal dynamics of association and previous studies on wild boar in north-eastern France (Poteaux et al. 2009) and free-ranging feral pigs in Texas, USA (Gabor et al. 1999).

The close match of the social structure revealed in social units and family groups suggests that they mirror the same level of social organisation. Social relationships of many

social species are hierarchically structured (African elephant: Wittemyer et al. 2005; Galapagos sea lion: Wolf et al. 2007; bottlenose dolphins: Wiszniewski et al. 2009; review in Hill et al. 2008). Levels of social organisation help individuals to cope with dynamic ecological and social pressures and can be determined by spatial isolation and habitat fragmentation (bottlenose dolphins: Lusseau et al. 2003, Wiszniewski et al. 2009), seasonality (African elephants: Wittemyer et al. 2005), sex and age of individuals (Wittemyer et al. 2005, Galapagos sea lions: Wolf et al. 2007), and finally individual ranging patterns, social preferences and kinship at the finest spatial scale (African elephants: Wittemyer et al. 2005, Galapagos sea lions: Wolf et al. 2007, Wolf and Trillmich 2008). Apparently, at the spatial scale of the present study, there was no evidence for a hierarchical pattern in wild boar social organisation. Nonetheless, high intra-group relatedness, cohesion, and stability suggest that social units represent a basic functional level of wild boar social structure. A similar pattern is observed in matrilineal societies of African elephants (Wittemyer et al. 2005, Archie et al. 2006).

The social network of the studied wild boar population was spatially structured. Space utilised by the members of a given social unit overlapped extensively, while little overlap was observed between individuals across social units. Spatial segregation appears to be a common rule of social structuring in many species. However, genuine social preferences often override spatial relationships proving that observed structures are not mere effect of individuals distribution in space (Lusseau et al. 2006, Wolf et al. 2007, Wiszniewski et al. 2009, Mourier et al. 2012). Is this the case also in the studied wild boar population? Naturally, since spatial extent of the study site greatly exceeded the average home range size, we should expect individuals in close proximity to interact more often. Not surprisingly, wild boar associations and spatial overlap were found to correlate. The majority of marked individuals (82%) showed some overlap and thus, potentially, they had the chance to interact. However, only 26% of animals associated at least once. Moreover, some pairs of individuals sharing as much as 40-50% of utilised area did not form associations, and some pairs associated infrequently (half-weight association index  $\leq 0.22$ ) despite extensive spatial overlap of their utilised area (66-79%). Finally, genetic data showed that preferential, kin targeted, associations persisted in the population regardless of spatial proximity. Consequently, spatial distribution and overlap of individuals does not fully explain association patterns, what indicates that active choices made by animals played an important role in shaping social structure of the studied population. Comparable mechanisms were found to drive complex structures of bottlenose dolphin societies (Lusseau et al. 2006, Wiszniewski et al. 2010).

Fine-scale site fidelity creates an environment that facilitates development of social relationships through repeated, non-random interactions. It can also favour and reinforce cooperative behaviours and behavioural reciprocity (as shown by theoretical work of Ferrière and Michod, 1996), leading to strong bonds between some animals. Site fidelity occurring over generations (through limited dispersal and home range inheritance) leads to local clustering of kin or matriline (grey seals *Halichoerus grypus*: Pomeroy et al. 2001; Canada geese *Branta canadensis*: Fowler 2005; Australian sea lion *Neophoca cinerea*: Campbell et al. 2008). In such a scenario, likely to be present in wild boar, increased indirect fitness benefits make strong social bonds between relatives particularly rewarding (Townsend's voles: Lambin and Yoccoz 1998; yellow-bellied marmots: Armitage and Schwartz 2000, Canada geese: Fowler 2005; review in Silk 2007). Yet, the question remains how animals choose social partner, which in turn leads to the formation of these stronger bonds. In populations organised in kin clusters, kin discrimination is a prime candidate for mechanism determining choice of social partner (theoretical work of Perrin and Lehmann 2001; grey seals: Pomeroy et al. 2001). Queller (1992) suggested that a mechanistic, spatially based rule can be sufficient to recognize kin. It assumes that individuals in the natal area are likely relatives and allow animals to infer from this probability when making behavioural decisions. My results show that kin-directed social preferences in wild boar extend beyond simple spatial proximity and thus imply the potential role of kin recognition.

Wild boar within the same social units were more related to each other than to members of other social units. Compared to family groups, the average intra-unit levels of relatedness were lower probably due to social unit composition, i.e. admixture of unrelated solitary individuals, mix of few families. Nevertheless, a similar pattern of strong genetic structuring in family groups and social units confirms that they represent virtually the same level of wild boar social organisation. Consequently, parallel mechanisms and adaptive values, as discussed for family groups, also apply to the formation and persistence of social units. High intra-unit relatedness among adult females supports the matrilineal nature of the social units.

On the contrary, adult males and adult females associated in the same social units were not related. However, adult boars (males) normally do not form stable associations with groups (this study, and southern France: Dardaillon 1988; central Italy: Boitani et al. 1994; feral pigs in the USA: Gabor et al. 1999). It is possible that males may interact preferentially with a group of breeding females before mating season to increase their mating opportunities

later on. As observations of adult males associating with groups were rare, they may represent an alternative male mating strategy.

### **5.5.2. Variation in sociality within the network**

Sociality of wild boar, estimated by three network centrality measures, varied primarily with age of individuals. A general decrease in the level and diversity of social connectivity throughout the lifetime of an individual was also modified by its sex. The degree of sociality during an individual's lifetime may change as a behavioural response to different life stages. Young wild boar of both sexes remain in their natal groups from birth until roughly 1.5 year of age, when dispersal occurs. Adult females recruit into natal matriline or settle in their close vicinity, whereas adult males become solitary (Dardaillon 1988, Boitani et al. 1994, Cousse et al. 1994, Gabor et al. 1999, Kaminski et al. 2005, Poteaux et al. 2009, Keuling et al. 2010, this study). These life-history patterns were largely mirrored in changes of sociality at different life stages.

Young wild boar had the strongest connections within the network. As those animals were in pre-dispersal age, their high strength most likely reflected strong bonds within natal groups. This is consistent with extended intra-group associations reported previously (Kaminski et al. 2005). The onset of dispersal marked a decrease in the strength of social connections. Dispersing and adult males showed the weakest connectivity, which conform to their solitary lifestyle and temporally limited association rates as shown previously. Interestingly, adult females showed a weaker association strength compared to yearlings, suggesting a lower intensity of intra-group contacts between adult females and yearlings than among yearlings. Strong bonds among yearlings might facilitate dispersal decisions which, were observed to be synchronised within the natal groups (Kaminski et al. 2005).

Yearlings were overall best connected within the social network suggesting that diverse associations extend beyond strong bonds within their natal groups. Such behaviour could potentially precede and facilitate dispersal decisions by allowing animals to assess habitat quality and social context in the vicinity of the natal area. Extensive exploratory behaviour in the yearling wild boar was described by Cousse et al. (1994) in southern France.

Older females showed a gradual decrease in the diversity of connections, probably due to strong site-fidelity and low inter-group interactions of adult females as demonstrated by lagged association rates. Adult males were least connected within the network indicating their occasional social interactions. Nevertheless, eigenvector centrality showed very high variation across age classes, suggesting that other factors could influence individual variation in sociality, one of the candidates being characteristics of behavioural traits of individuals

(personalities or temperaments) (Krause et al. 2010). Behavioural signatures of individuals have been shown to affect individual social relationships in rhesus macaques *Macaca mulatta* (Weinstein and Capitanio 2008) and connectivity within social network in three-spined sticklebacks *Gasterosteus aculeatus* (Pike et al. 2008) and guppies (Croft et al. 2009).

The tendency to group, as measured by clustering coefficient, was the highest among yearling wild boars. This is in accordance with other findings of this study demonstrating temporal and spatial cohesion of the family groups. Grouping tendency decreased with age and showed marked, yet statistically insignificant, intersexual differences. Female's clustering coefficient tended to decrease only slightly until adulthood indicating their role in building social groups as demonstrated in this and previous studies (Gabor et al. 1999, Kaminski et al. 2005, Poteaux et al. 2009). Conversely, males' tendency to group declined sharply as they grew older. Overall, however, the clustering coefficient decreased with age of individuals reflecting a gradual shift from strong intra-group relationships in young animals to increased number of interactions directed outside the group in older ones. Age has been identified as a strong predictor of an individual's sociality and association structure in females of rhesus macaques (Widdig et al. 2001) and baboons *Papio cynocephalus* (Silk et al. 2006) and in males of African elephants (Evans and Harris 2008).

All three centrality measures used in the present study highlighted the role of young wild boar in maintaining cohesion of the social network. This was also evident from a higher mean association index and overall network connectivity in year 2008, when yearlings made up 53% of the sampled individuals, compared to 2009, when yearlings were nearly absent (3%). Altogether, two explanatory variables (sex and age) explained changes in sociality reflecting major transitions in wild boar ontogeny. Yet, identifying the behavioural and ecological mechanisms shaping the architecture of social networks in this species requires future research.

This study, by comprehensive methodological approach, showed how behavioural decisions of an individual translate into emergent social and genetic structure at the population level. Structural properties of the social system revealed in social network were confirmed by trapping and genetic data. Moreover, spatial and genetic information provided evidence that preferential, kin-targeted, interactions of females underlay observed social organisation. Such detailed insights would not have been possible using just one of the employed methods. This methodological approach appears particularly suited to study how kin selection shapes and operates at different levels of animal social systems.

## 6. CONCLUSIONS

(1) Social organisation of the wild boar population in Białowieża Primeval Forest was generally shaped by non-random, preferential associations, which were largely stable and long-lasting. High temporal stability of associations observed among animals forming groups implies strong group cohesion. Consequently, fission-fusion dynamics was moderately low. Positive correlation between strength of social bonds and genetic relatedness extended beyond the effect of spatial proximity of individuals. However, kin-targeted interactions were observed only among females. Adult males engaged in dynamic, short-lived relationships.

(2) Family group, determined from trapping and genetic data, was typically composed of 1-2 adult females, several yearlings and few subadults and, on average, consisted of 7 individuals. Most adult males were solitary. Group composition was largely shaped by kinship. Mean intra-group level of relatedness corresponded to second-degree relatives. Extensive spatial overlap was observed among animals within groups, and limited overlap across groups. This is indicative of the significant group effect on space use patterns and strong site fidelity.

(3) Social structure of the wild boar population, revealed by network analysis, trapping, and genetic data, was organised in well-defined and cohesive social units. The units were also genetically distinct, with high intra-group and low inter-group genetic relatedness. The genetic structure in the network can be interpreted as an emergent property of philopatry and spatial segregation of social groups. However, spatial relationships could not fully explain association patterns and network structure. The importance of social preferences and kin-targeted interactions was apparent, particularly among females.

(4) Sociality of wild boar generally decreased with the age of individuals. Magnitude of the effect was modified by sex. Young wild boar showed the strongest grouping tendency and were the most diversely connected within the network. The onset of dispersal marked a decrease in sociality, which was manifested stronger in males than in females. These results highlight the role of young wild boar in maintaining cohesion of the social network.

(5) Genetic and behavioural data revealed a limited spatial extent of wild boar dispersal and strong kin-based structuring of the population. Sex bias in dispersal frequency was insignificant. Females usually settled in the direct vicinity of the maternal home range and males few home ranges away from the natal site. Spatial genetic structure was detected at a small spatial scale corresponding to few home ranges in the studied population.

(6) The study showed how social and genetic structure of the population emerge from behavioural decisions and preferential interactions of individuals.



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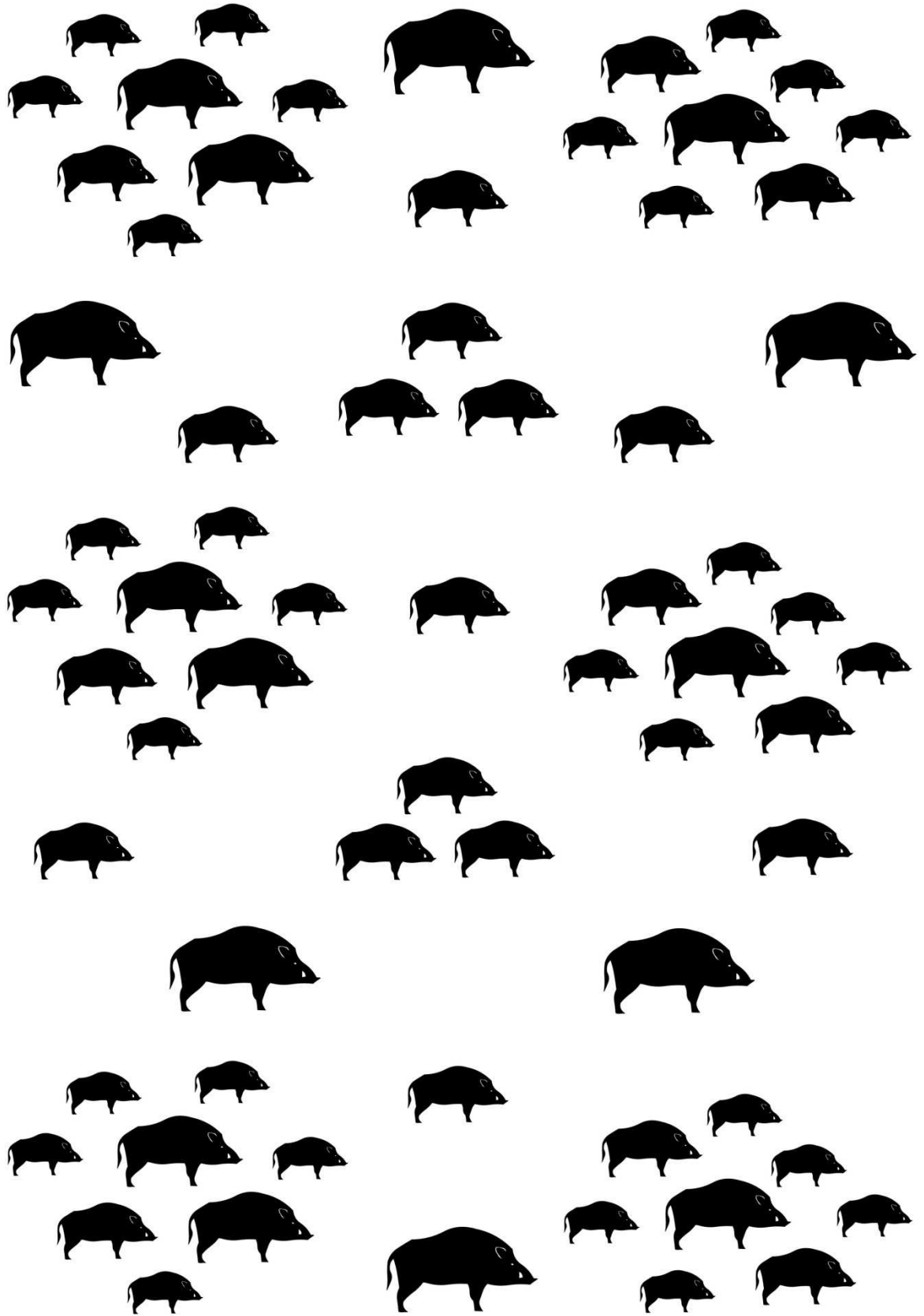
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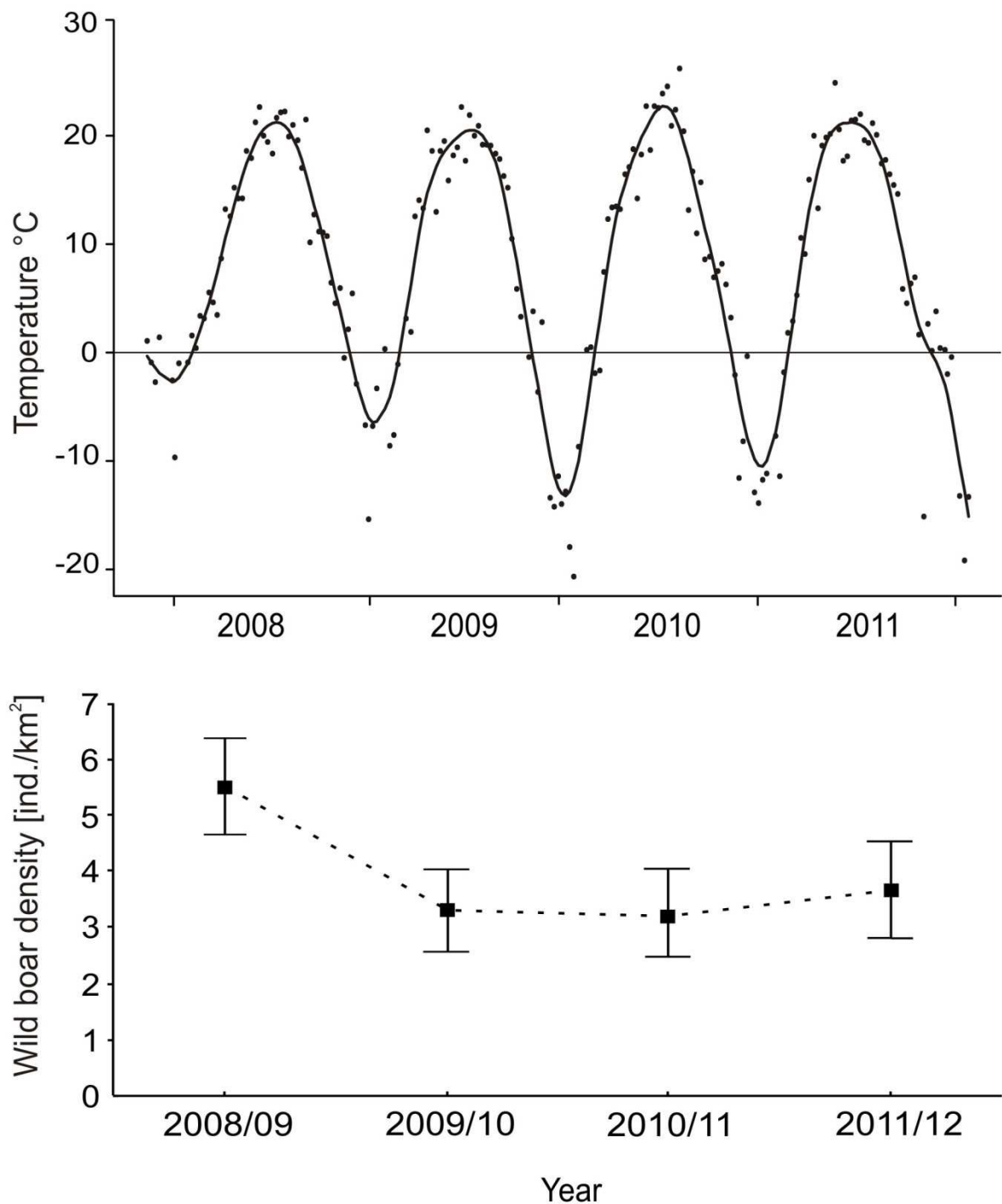
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## Appendix 1. Temperature and wild boar density dynamics

Fig. A. Temporal variation of the temperature record (upper panel) and wild boar population density (lower panel) within the study area (central part of the Białowieża Primeval Forest). Eight-day temperature record was obtained from MODIS data sets (<http://modis.gsfc.nasa.gov/>). Estimates of wild boar density come from annual drive-counts conducted in January-February (unpublished data of the Mammal Research Institute, Polish Academy of Sciences).



## Appendix 2. Models describing temporal patterns of wild boar associations

Table A. Models of lagged association rates among all individuals as well as within and between sexes of adult wild boar in Białowieża Primeval Forest. Each model consists of a proportion of constant companions (CC,  $p_{cc}$ ), rapid disassociations (RD), and casual acquaintances (CA) of two types: short-term ( $p_{ca}$ ) that last for particular period of time ( $\tau_{ca}$ ), and more permanent acquaintances ( $p_{perm}$ ) lasting for longer periods ( $\tau_{perm}$ ). The standard error (SE) of each parameter (given in parentheses) was estimated by jackknifing procedure. For a more detailed description of the models see (Whitehead 1995).

Model of association	$p_{cc}$ ( $\pm$ SE)	$p_{ca}$ ( $\pm$ SE)	$\tau_{ca}$ (-SE, +SE)	$p_{perm}$ ( $\pm$ SE)	$\tau_{perm}$ (-SE, +SE)
All – All Two levels of CA $g(d) = p_{ca} e^{-(d/\tau_{ca})} + p_{perm} e^{-(d/\tau_{perm})}$	-	0.31 (0.09)	0.9 days (0.50 – 4.81)	0.69 (0.09)	3.7 years (1.61 – 9.13)
Female – Female CC + CA + RD $g(d) = p_{cc} + p_{ca} e^{-(d/\tau_{ca})}$	0.81 (0.09)	0.10 (0.06)	7.1 days (4.42 – 18.43)	-	-
Male – Male CC + CA + RD $g(d) = p_{cc} + p_{ca} e^{-(d/\tau_{ca})}$	0.06 (0.01)	0.34 (0.21)	2.8 days (1.99 – 4.65)	-	-
Male – Female CC + CA + RD $g(d) = p_{cc} + p_{ca} e^{-(d/\tau_{ca})}$	0.002 (0.006)	0.24 (0.21)	2.9 days (1.12 – 4.85)	-	-

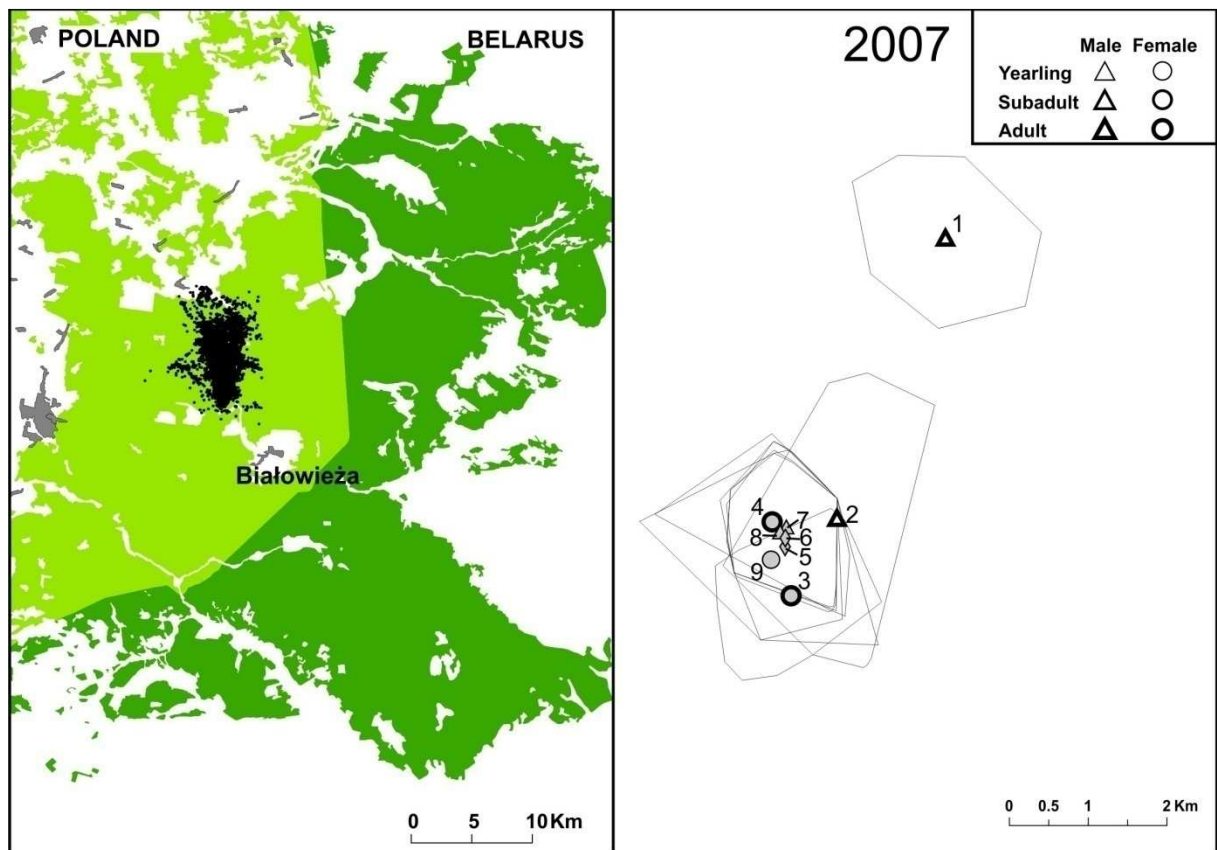
Table B. Models fit to standardized lagged association rate (SLAR) describing temporal association patterns among all radio-marked animals, within yearlings/subadults, and between yearling/subadult and adult wild boar in Białowieża Primeval Forest. The best fitting model was chosen by minimising quasi-Akaike Information Criterion value (qAIC). Standardized association rate,  $g(\tau)$ , is given as a function of time lag,  $\tau$ . The standard error (SE) of each parameter (given in parentheses) was estimated by jackknifing procedure. For a more detailed description of the models see Whitehead (1995).

Model of association	$a_1$	$a_2$	$a_3$	Duration of association
<b>All - All</b>				
Casual acquaintances <sup>1</sup>	0.00051 (0.00043)	0.223 (0.015)	-	5.35 years (2.92 – 31.93)
	$g(\tau) = a_2 e^{(-a_1\tau)}$			
<b>Yearling/subadult – Adult</b>				
Constant companions + Casual acquaintances	0.02479 (0.02783)	0.499 (0.040)	0.104 (0.083)	40.34 days (19.00 – 328.08)
	$g(\tau) = a_2 + a_3 e^{(-a_1\tau)}$			
<b>Yearlings/subadults</b>				
Casual acquaintances <sup>1</sup>	0.00026 (0.00036)	0.277 (0.01)	-	10.74 years ( 4.43 – 25.21)
	$g(\tau) = a_2 e^{(-a_1\tau)}$			

<sup>1</sup>Duration of these relationships estimated by the model indicate their long-term and stable character, corresponding to constant companionships.

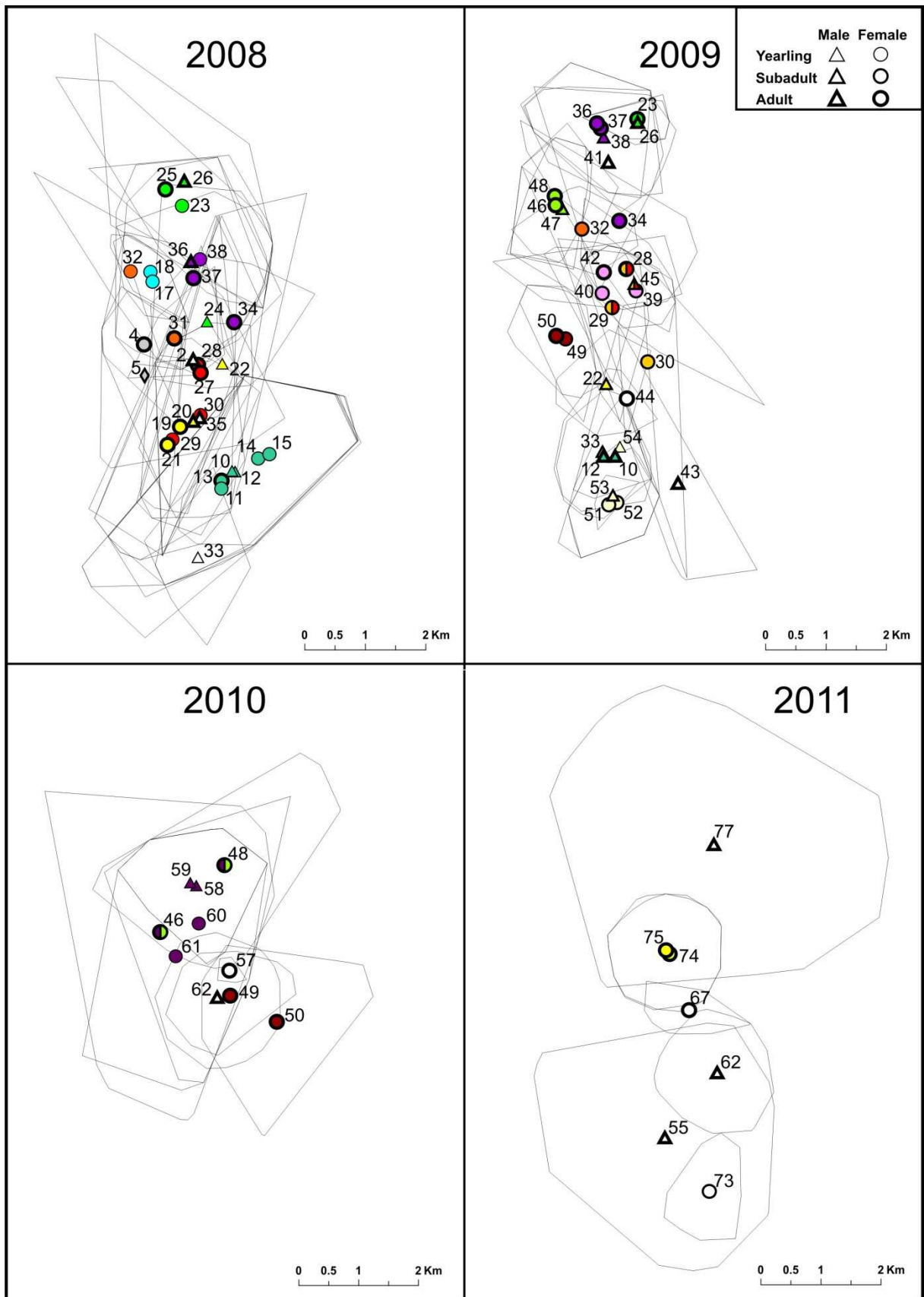
### Appendix 3. Spatial distribution and social organisation of telemetry-marked wild boar

Fig. A. Maps detailing spatial distribution of telemetry-marked wild boar within the study area in 2007-2011. The first map shows the study area (with black dots indicating telemetry locations) located in the centre of the Polish part of Białowieża Primeval Forest. The following maps present spatial organisation of the telemetry-studied wild boar. Symbols and identity numbers represent individuals (location of the home range centroid). Colour of the symbols refers to family group membership (the same colour for one group, double-coloured symbols refer to individuals re-trapped in another group, colourless symbols indicate solitary animals). Polygons represent 90% Minimum Convex Polygon home-range estimates.



Appendix 3. – continued on the next page

Appendix 3 – concluded.



#### Appendix 4. Long-distance movements of marked wild boar

Fig. A. Long-distance movements of subadult and adult wild boar determined by radio-tracking and feedback from hunters. Red lines indicate straight-line distance from the capture site to the location, where the individual was last recorded.

