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Research Article

Contact Rates in Wild Boar Populations: Implications for Disease Transmission

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ABSTRACT Inter-individual contacts in wildlife populations are usually highly heterogeneous. This variation translates into differential disease transmission rates between individuals, which have vital consequences for the spread, persistence, and control of infectious diseases. Wild boar (*Sus scrofa*) is an abundant game species across Europe that poses serious health threats to wildlife, livestock, and humans. However, factors shaping contact rates and structure in wild boar populations, key parameters in disease ecology, remain poorly studied. We quantified dyadic association rates, as a proxy of contacts, and individual-based network centrality measures using telemetry data from 3 wild boar populations across Europe. Next, we examined the effect of sex, age, group membership, and space use on association rates and individual centrality. Contact rates depended strongly on the distance between individual home ranges; the most frequent associations occurred at distances of 0–1 km (mostly within groups), less frequent at 1–3 km (mostly between groups), and sporadic at >4 km. Association rates were an order of magnitude higher within social groups than between them. Between-group association rates were only dependent on the distance between groups, with no apparent effect of animal sex or age. At the social network level, young animals (0.5–2 yr) showed greater between-group connectivity and a more central position in the network than adults. Our results highlight substantial contact heterogeneities in wild boar populations, which should be considered in epidemiological modeling and disease control actions. First, wild boar contact rates are strongly constrained socially and spatially. Hence, management measures reducing these constraints, such as supplementary feeding and intensive hunting, may lead to increased disease transmission rates. Second, young wild boars show exceptional connectivity within the population, highlighting their high capacity for disease transmission. Therefore, targeted removal of yearlings should be considered to optimize disease control efforts. © 2018 The Wildlife Society.

KEY WORDS centrality, contact heterogeneity, disease ecology, social network, *Sus scrofa*, telemetry.

Contact among individuals is a key element in the dynamics of any directly transmissible disease. In most wildlife populations, contacts are structured socially or spatially and this variation in contact rates among individuals can affect probability, size, and persistence of disease outbreak (Lloyd-Smith et al. 2005, Bansal et al. 2007). The type of social system can thus affect the rate and mechanisms of disease spread (Altizer et al. 2003). For example, in animal societies with closed social structure, individual contacts and pathogen transmission is largely contained within social groups, potentially limiting disease spread (Cross et al. 2005, Grear et al. 2010). Spatial proximity between individuals can also shape contact frequency (Davis et al. 2015) and resulting spatial structuring of contacts may limit the speed at which disease spreads in the population (VanderWaal et al. 2013). Therefore, understanding the social patterns and spatial constraints of contacts among individuals is important for predicting disease dynamics and its effects on host populations.

Analysis of animal social network is often a tool of choice in studies of contact heterogeneity and its role in pathogen transmission. This approach enables biologists to identify highly connected individuals that have particularly high chances of acquiring and shedding diseases (Lloyd-Smith et al. 2005, Weber et al. 2013), determine population structure, and identify individuals responsible for linking different components of the network (Weber et al. 2013, VanderWaal et al. 2016). Because different factors may act on each level of social organization (Vander Wal et al. 2016), a hierarchical approach combining analysis of dyadic associations and network-based metrics, as adopted in our study, offers full understanding of the factors influencing contact heterogeneity (Pepin et al. 2016, Vander Wal et al. 2016).

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Information about contact rates and structure in wildlife populations can be used to parameterize epidemiological models (Craft et al. 2011, Pepin and VerCauteren 2016) and inform disease management to optimize targeted control actions (Grear et al. 2010, Hirsch et al. 2016).

Wild boar (*Sus scrofa*) is an abundant game species across Europe (Apollonio et al. 2010) that poses serious health threats to wildlife, livestock, and humans. Among many parasitic, viral, and bacterial pathogens carried by wild boar, there are causative agents of economically devastating livestock diseases, such as classical and African swine fever (Rossi et al. 2005, Costard et al. 2013), and zoonoses, such as brucellosis, hepatitis B, and leptospirosis (Vicente et al. 2002, Meng et al. 2009, Caruso et al. 2015). The capacity of wild boar populations to spread infectious diseases is further amplified by rapidly increasing densities throughout Europe (Massei et al. 2015) and colonization of urban areas (Stillfried et al. 2017). Given these facts, it is surprising how little is known about factors shaping contact rates and structure in wild boar populations, which are key parameters in disease ecology. A few studies investigating association patterns in wild boar revealed positive effects of female kinship and spatial proximity between individuals on the strength of social bonds (Gabor et al. 1999, Kaminski et al. 2005, Podgórski et al. 2014*a*). These studies did not, however, explicitly quantify contact rates to decouple the role of social (group membership), spatial (distance between individuals), and demographic (sex and age classes) effects in shaping variation in contacts. A recent study from across the United States (Pepin et al. 2016) attempted to fill these knowledge gaps and reported strong social and spatial structuring of contact rates among feral pigs. However, these results, obtained from non-native feral pig populations, may not be fully translatable to the European context, where wild boar occur naturally.

Our objective was to quantify association patterns in 3 European populations of wild boar to determine social, spatial, and demographic factors affecting dyadic association rates; estimate individual connectedness within the social network and determine factors influencing individual-based network centrality measures; evaluate differences in factors influencing dyadic associations and individual-based network centrality measures; and provide spatial and demographic parameters for epidemiological modeling and disease management. We expected to observe a positive effect of spatial proximity and shared group membership on the contact rates. We hypothesized that young animals, because of their increased mobility during dispersal, would exhibit higher contact rates and better connectivity in the population.

STUDY AREA

Data used in this study were collected in 3 wild boar populations originating from 1) Białowieża Primeval Forest (BPF), eastern Poland (52°47′N, 23°48′E); 2) Mecklenburg-Western Pomerania (MWP), northern Germany (53°28′N, 10°55′E); and 3) Alpe di Catenaia (AdC), central Italy (43°48′N, 11°49′E). The BPF was a 600-km^2 continuous forest complex that is the last remnant of the European temperate lowland forest. The MWP is 70 km^2 of lowland agriculture characterized by oceanic climate. The area is comprised of 40% farmland, 34% forest, 23% pastures and meadows, and 3% estates. The AdC is a 120-km^2 mountainous area with elevation ranging from 490 m to 1,414 m above sea level and temperate climate with marked seasonality. Forests covered 85% of the study area and the remaining 15% consisted of shrublands, agricultural land, and estates. More detailed description of the study sites are provided by Keuling et al. (2008), Iacolina et al. (2009), and Podgórski et al. (2014*a*) for MWP, AdC, and BPF, respectively.

METHODS

Live-Trapping and Telemetry

We captured wild boar using cage traps (BPF: Podgórski et al. 2014*a*; MWP: Keuling et al. 2008; AdC: Iacolina et al. 2009), drop-net traps (BPF: Jędrzejewski and Kamler 2004), vertical nets (AdC: Iacolina et al. 2009), or the combination of those (BPF, AdC). Upon capture, we determined the sex and age of animals based on teeth eruption and wear patterns (Matschke 1967, Briedermann 1986). We classified animals into 3 categories: juveniles (<12 months), yearlings (12–24 months), and adults (>24 months). Because the marked juveniles were older than 6 months and we were mostly interested in the behavior of dispersing animals, we merged the first 2 categories into 1 (yearlings) for further analysis to cover the dispersal age (Podgórski et al. 2014*b*). We fitted captured animals with ear tag radio-transmitters in BPF (Advanced Telemetry Systems, Isanti, MN, USA and Wagener Telemetrieanlagen, Cologne, Germany), MWP (Wagener Telemetrieanlagen), AdC (TXP-R, Televilt, Lindesberg, Sweden), and radio-collars (TXV-10, Televilt) in AdC. We surveyed the study areas 2–6 times per week, with equal intensity during day and night, and attempted to locate all marked animals within 1 day. Further details on the trapping and tracking protocol are provided by Keuling et al. (2008), Iacolina et al. (2009), and Podgórski et al. (2014*a*) for MWP, AdC, and BPF, respectively. The research and handling protocols conformed to legislation regarding wildlife and animal welfare of the respective countries and were approved by the relevant authorities (MWP: Ministry of Agriculture Mecklenburg-Western Pomerania, Germany, and Landesamtes für Landwirtschaft, Lebensmittelsicherheit und Fischerei [LALLF] Mecklenburg-Vorpommern, Germany [permit number LVL-MV310-4/7221.3-1.1-032/01]; AdC: Administration of the Region of Tuscany, Italy [decision number 103/5936/152 and 123/5828/152]; BPF: Ministry of Environment of the Republic of Poland [decision number DLgł-6713/12/08/ab], Białowieża National Park [permit issued on 8 Apr 2008], Local Ethical Commission for Experiments on Animals in Białystok, Poland [resolution number 19/2008]).

Data Analysis

We considered 2 individuals to be associated if they were located simultaneously (<1 hr) within 200 m of each other.

This distance threshold allowed us to account for radio-tracking error, which ranged from 60 m to 150 m (Keuling et al. 2008, Iacolina et al. 2009, Podgórski et al. 2014*a*). We commonly observed wild boar groups spread over such distances, especially when foraging or traveling, and we assumed that direct contacts occur regularly among animals within this distance. The 200-m threshold was also more conservative than those previously used (Iacolina et al. 2009, Podgórski et al. 2014*a*). We quantified the strength of dyadic associations with the half-weight index (HWI; Cairns and Schwager 1987) in SOCPROG 2.4 (Whitehead 2009). The HWI ranges between 0 (2 individuals never located together) and 1 (2 individuals always located together). We set the sampling period to 1 day to mirror the actual sampling schedule. We used pairwise HWI matrices to construct and visualize weighted networks using NETDRAW (Borgatti 2002), which resulted in giant components of 30, 20, 27 interconnected individuals in BPF, MWP, and AdC, respectively. We determined structure of the populations from association data by finding an optimal subdivision of the social network into several clusters using modularity matrix clustering (Newman 2006) as implemented in SOCPROG. This method finds optimal network structure through an iterative process of dividing the network into 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 quantified by the modularity index Q. The most parsimonious division in the network (the one maximizing Q) provides the most edges within clusters and the least between. We verified groupings based on network clustering with trapping data, telemetry, and field observations. Specifically, we assumed that individuals captured together or moving together during the first month after capture belonged to the same social unit. Social units resulting from field data and partitioning of the social network corresponded with each other in most cases (Table S1, available online in Supporting Information). We used network-based clusters as equivalents of social groups in further analyses for methodical consistency among sites.

We calculated 6 individual-based measures of social network centrality that may be important for disease transmission. Degree quantified number of associates (links) of the focal individual, whereas strength additionally accounted for the weight of these links (i.e., frequency of associations). The next 2 measures separately calculated degree and strength for each focal individual with animals outside of its social group only, hereafter between-group degree and between-group strength, respectively. Other studies have highlighted the importance of between-group contacts for infection risk and disease spread (Weber et al. 2013, VanderWaal et al. 2016). We normalized strength and degree across networks (dividing the measure by $N-1$, where N was the number of nodes in the network) to account for differences in the sample size between populations. The other 2 measures, betweenness and closeness, quantified indirect connectivity of the focal individual. Betweenness measures the number of shortest paths going through an individual linking other individuals in the network; high values characterize individuals with a large potential to transfer diseases in the network (i.e., super-spreaders; Lloyd-Smith et al. 2005). Closeness is an average length of shortest paths connecting the focal individual with all others in the network and corresponds to the time it takes to spread the disease from 1 individual to all others. The closer the individual is to all others, the more central its position in the network. We used weighted versions of betweenness and closeness, as implemented in R-package tnet (Opsahl 2009), with the alpha parameter set at 0.5 to balance the contribution of the number and weight of ties to these measures (Opsahl et al. 2010).

Statistical Analysis

To evaluate which factors shaped association rates and network centrality measures, we performed linear mixed-effects models (Pinheiro and Bates 2000). We investigated variation in association rates for overall dyadic HWI, within-group dyadic HWI, and between-group dyadic HWI. We included data only from pairs of individuals that associated at least once ($\text{HWI} > 0$). Explanatory variables included age similarity (yearling–yearling, adult–adult, yearling–adult), sex similarity (female–female, male–male, female–male), distance between home range centroids (calculated as median of longitude and latitude from all locations of the individual), and group membership (animals belonging to the same or different groups). Random factors included identities of both interacting individuals (to control for repeated observations) and study area (to control for unexplained variation among sites).

In the group of models investigating variation in the 6 network centrality measures, we tested the effects of an individual's age, sex, group size, home range size (90% minimum convex polygon), and its spatial marginality (mean distance of individual home range centroid to all other home range centroids). We included group identity and study area as random factors. We logit-transformed all response variables prior to model fitting if the transformations improved normality and reduced skewness as evaluated by visual inspection of the normal quantile plots of the residuals. Each full model included an interaction between sex and age. We computed mixed models using the lme4 package (Bates et al. 2015).

For both analyses, we performed backward stepwise model selection using the dropterm function from the R-package MASS (Venables and Ripley 2002). We sequentially removed the least significant terms from the full model until we minimized the Akaike's Information Criterion (AIC) and thus obtained the most parsimonious model. We quantified variation explained by the final models with conditional and marginal R^2 (Nakagawa and Schielzeth 2013) using the MuMIn R-package (Bartoń 2016). We performed all statistical and spatial analyses in R 3.3.2 (R Development Core Team 2015).

RESULTS

Association Rates

We obtained 2,469 radio-locations from 30 animals followed during 2008–2009 in BPF, 7,916 locations from 20 animals followed during 2003–2004 in MWP, and 2,629 locations from 27 animals followed during 2003–2004 in AdC. Radio-tracking periods lasted 12.6 ± 0.9 ($\bar{x} \pm$ SE) months in BPF, 11 ± 0.9 months in MWP, 11.1 ± 1.1 months in AdC, and overlapped among all animals in each study area by ≥2 months. There was a strong negative relationship between the distance of home range centroids and frequency of associations in pairs of individuals within and between social groups (Fig. 1, Table 1). Most of the recorded associations (71.2%) occurred between animals living close together (home range centroids <1 km), 24.6% occurred among animals separated by 1–3 km, and 4.2% occurred between pairs separated by >3 km. There was a significant social structuring of associations rates. Individuals within groups associated much more frequently than between groups (HWI = 0.59 ± 0.02 and 0.035 ± 0.002, respectively; Fig. 1, Tables 1 and S1). The relationship between-group size and within-group HWI was positive but statistically not significant (coefficient = 0.017 ± 0.016, $P = 0.329$). As group size increased from 2 to 11 individuals, mean HWI within groups increased from 0.48 to 0.69 (Table S1). Within-group interactions were short-range; 87% of them occurred between animals with home range centroids at <0.5 km, 95% occurred within 1 km, and none occurred when home ranges were >2 km apart (Fig. 1). The best-fit model for within-group associations predicted a 53% decline in HWI over a range of 0–1 km (Fig. 1). Between-group contacts occurred over longer distances (Fig. 1). Spatial proximity was the sole variable explaining variation in the frequency of inter-group associations (Table 1). According to the model estimates, HWI of animals from different groups decreased at a rate of 29% with every 0.5 km of distance between their home range centroids, declining by an order of magnitude between 0.5 km (HWI = 0.033) and 4 km (HWI = 0.003; Fig. 1). Between-group associations were the most frequent at a distance <1 km (57% of all 236 between-group dyads), less frequent at 1–3 km (36% of dyads), and sporadic at >3 km (7% of dyads). Only 3 of 94 observed dyads that were separated by 4–6 km came into contact at least once and there were no contacts beyond 4.5 km. Association frequency among yearlings (HWI = 0.34 ± 0.02, $n = 213$) was higher than between yearlings and adults (0.12 ± 0.02, $n = 130$, $P = 0.013$) and marginally higher than among adults (0.12 ± 0.04, $n = 34$, $P = 0.054$; Table 1). The effect of age similarity, with similar trends, was significant in the best model for within-group associations only but did not help explain variation in between-group contact rates (Table 1). The effect of sex similarity was not significant in the full models explaining variation in overall HWI ($F_{2,158} = 0.73$, $P = 0.48$), within-group HWI ($F_{2,77} = 0.53$, $P = 0.59$), or between-group HWI ($F_{2,121} = 1.19$, $P = 0.31$), and we dropped it early in the model selection process.

Network Centrality Measures

The proportion of the animals in the network associating with the focal individual (i.e., normalized degree) was higher in young animals (0.45 ± 0.025) than in adults (0.32 ± 0.034; Figs. 2 and 3, Table 2). Young wild boar also tended to have more associates from outside of their own social group (i.e., higher between-group degree) than adults (Fig. 2, Table 2). Both overall degree and between-group degree were related to the spatial position of the individual and group size. Individuals with more peripheral placement of the home range had fewer social partners (Fig. 2, Table 2), whereas

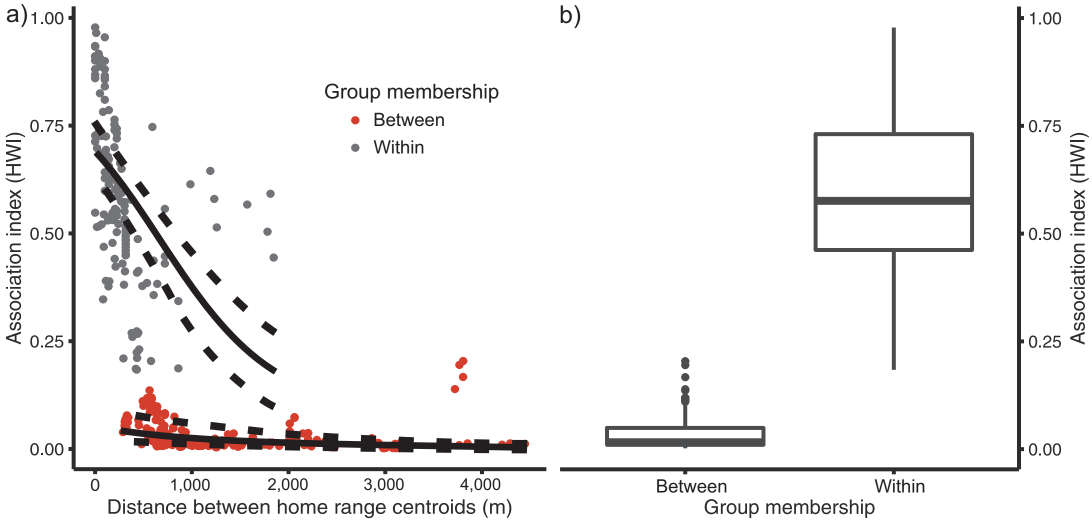

Figure 1. Socio-spatial structure of the association rates in wild boar populations from Germany (2003–2004), Italy (2003–2004), and Poland (2008–2009). We present the relationship between the pairwise half-weight association index (HWI) and spatial distance between home range centroids among animals belonging to the same (in gray) and different (in red) social groups (a). Each dot represents a pair of individuals, solid lines represent the effect of spatial distance from the linear mixed-effects models explaining variation in HWI and dashed lines represent 95% confidence limits around the model estimates. We also show the difference in HWI between animals from the same and different social groups (b).

Table 1. Variables included in the most parsimonious models explaining variation in dyadic association rates of wild boar, measured by half-weight index (HWI) in populations from Germany (2003–2004), Italy (2003–2004), and Poland (2008–2009). We built 3 separate models for association rates among pairs of individuals within groups, between groups, and overall in the wild boar populations. We fit response variables (all logit-transformed) with linear mixed-effects models with identities of both interacting individuals and study area as random factors. Candidate explanatory variables included age similarity (yearling–yearling, adult–adult, yearling–adult), sex similarity (female–female, male–male, female–male), distance between home range centroids (continuous variable), and group membership (association within or between groups). The reference category for age was yearling–yearling and reference category for group membership was between-group.

Response variable	Parameter	n	R^2_{marginal}[a]	$R^2_{\text{conditional}}$[b]	β	SE	P
Within-group HWI		142	0.37	0.55			
	Intercept				1.12	0.43	0.005
	Age (adult–adult)				−0.66	0.37	0.081
	Age (yearling–adult)				−0.74	0.19	<0.001
	Spatial distance				−0.002	0.0003	<0.001
Between-group HWI		236	0.19	0.93			
	Intercept				−3.04	0.43	0.015
	Spatial distance				−0.0007	0.00007	<0.001
Overall HWI		378	0.81	0.91			
	Intercept				−2.87	0.28	0.002
	Age (adult–adult)				−0.46	0.24	0.054
	Age (yearling–adult)				−0.36	0.14	0.013
	Spatial distance				−0.0006	0.00007	<0.001
	Group membership (within)				3.47	0.13	<0.001

[a] Variance explained by fixed factors of the model, calculated according to Nakagawa and Schielzeth (2013).

[b] Variance explained by fixed and random factors of the model, calculated according to Nakagawa and Schielzeth (2013).

animals from larger groups tended to have more associates (Fig. 2, Table 2). The amount of time an individual spent associating with others (i.e., normalized strength) was higher in young animals than in adults (0.12 ± 0.013 and 0.04 ± 0.006, respectively; Fig. 3) and increased with group size (Table 2). The frequency of associations with individuals from other groups (i.e., between-group strength) varied with individual age and sex as indicated by a significant interaction term in the best-fit model (Table 2). Between-group strength was the highest in young males (0.013 ± 0.002) and decreased by 59% in adult males (0.005 ± 0.001), which had values comparable to yearling and adult females (0.008 ± 0.002 and 0.006 ± 0.001, respectively). Closeness among young wild boar was 38% higher than among adults (14.4 ± 0.74 and 10.4 ± 0.85, respectively) and was positively related to group size (Table 2). We found no evidence of a significant effect of our explanatory variables on betweenness, and our best model explained only 6% of variation in this parameter (Table 2), indicating that we failed to identify factors shaping this centrality measure.

DISCUSSION

Spatial Effects on Contact Rates and Structure

We found that distribution of individuals in space was one of the main predictors of contact heterogeneity in a wild boar population. Animals living close together had higher association rates than distant ones. Within-group interactions were short-ranged and mostly occurred within 0.5 km, whereas most of the between-group associations occurred within 3 km and only sporadically beyond this distance. These results correspond with daily movements and

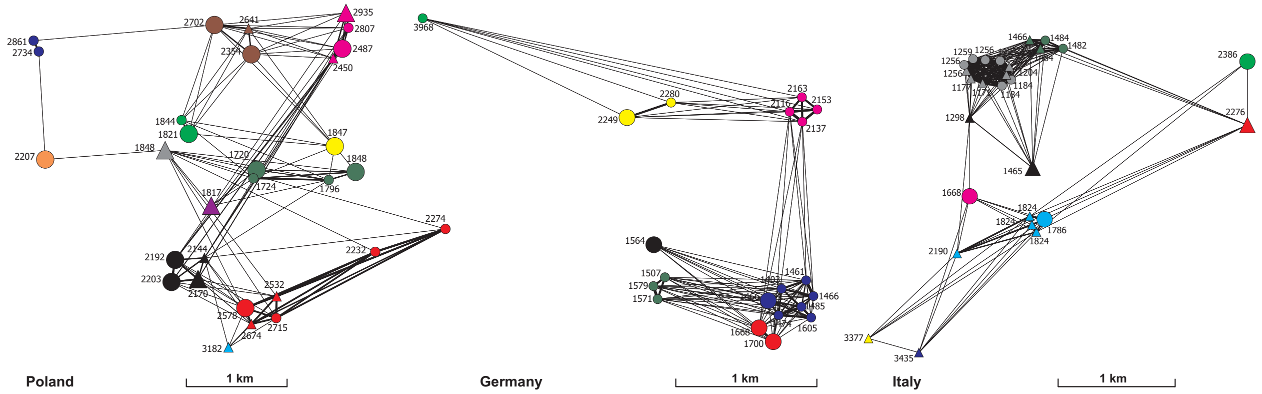

Figure 2. Socio-spatial networks of wild boar populations from Germany (2003–2004), Italy (2003–2004), and Poland (2008–2009). Nodes symbolize individuals, their colors represent social groups, size indicates individual age (small symbols = yearlings, large symbols = adults), and shape indicates sex (circle = female, triangle = male). All networks have spatial reference, with position of the node corresponding to the center of the individual home range and the node label showing its spatial marginality (i.e., average distance [in m] to all other individuals in the network).

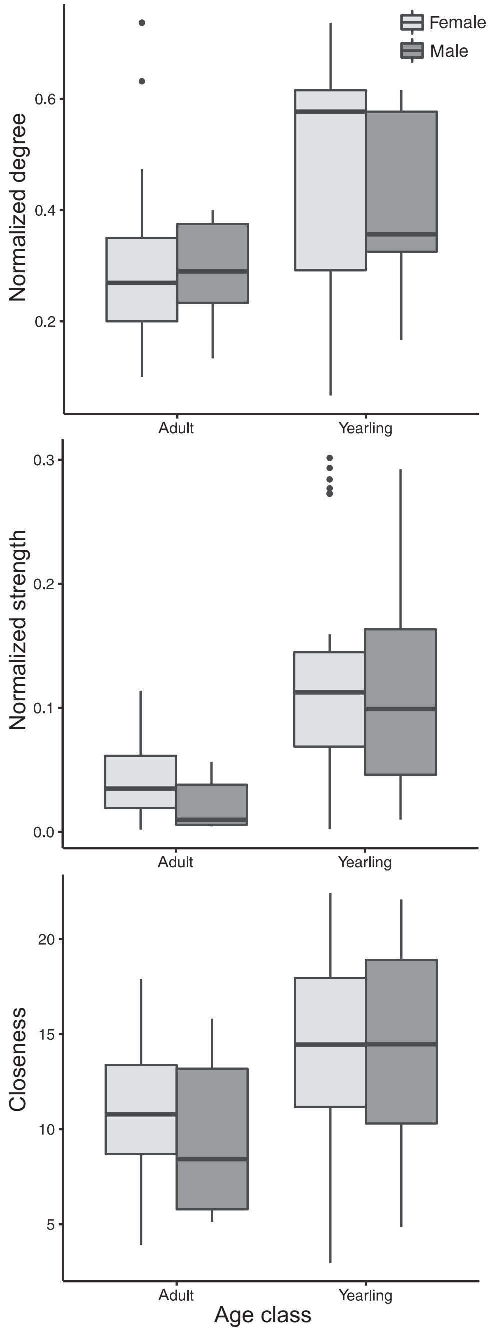

Figure 3. Effects of individual sex and age on 3 network centrality measures in wild boar social networks from Germany (2003–2004), Italy (2003–2004), and Poland (2008–2009).

typical home range sizes of wild boar (Keuling et al. 2008, Podgórski et al. 2013, Morelle et al. 2015) and are in general agreement with the spatial scale of between-group contacts found in feral pigs from the United States (Pepin et al. 2016). Spatial constraints on host contacts may reduce the rate of disease spread in the population, particularly for highly virulent and lethal pathogens (Cross et al. 2005). This mechanism could explain slow spatial spread of African swine fever in a wild boar population in Poland in 2014–2015 (Śmietanka et al. 2016).

Spatial arrangement of individuals can influence network structure and individual connectivity and impose spatial constraints on disease spread (Keeling 1999). We found that spatial position of the individual in the network correlated with the number of its social partners (degree; i.e., centrally placed animals tended to have more associates) even when we considered only between-group links. Because individual degree can correlate with infection risk (Drewe 2010, Godfrey 2013), our result highlights the greater opportunity for spatially central individuals to acquire and spread diseases. Notably, spatial position of the individuals in the network and the size of their home range had no significant effects on other network centrality measures considered (strength, closeness, betweenness). Thus, it appears that inter-individual distances and space use have stronger limiting effect on association rates at the dyadic level than on individual connectivity within the network.

Social Effects on Contact Rates and Structure

We found significant social structuring of contacts, with associations rates within groups 17-fold higher than among animals from different groups. Structuring of contacts can affect disease transmission patterns in the population and thus limit outbreak size (Cross et al. 2005). For example, the probability of acquiring chronic wasting disease from other members of a white-tailed deer (*Odocoileus virginianus*) matriline was >100-fold higher than from non-related females because of a higher intensity of within-group interactions (Grear et al. 2010). Our results indicate that infectious contacts will be much more frequent within wild boar groups than between them, imposing social constraints on disease transmission. Effect of these constraints on disease spread across the population will depend on pathogen characteristics, such as transmission route, infectiousness, incubation time, lethality. We can expect highly virulent pathogens with short infectious periods to spread rapidly within groups but have limited population-level effects, particularly in fragmented or low-density populations (Ward et al. 2009, Pepin and VerCauteren 2016).

Intensity of social contacts often differs among various classes of individuals in the population (Vander Wal et al. 2016). This variation can result in differential transmission risks and structured disease prevalence across the population, with important implications for management (Streicker et al. 2012). In our study, association rates among yearling wild boar were higher than with adults and among adults themselves. Additionally, age influenced most of the individual-based network centrality measures, with yearlings associating more often and with a greater number of individuals than adults and showing higher between-group connectivity. According to the strength of weak ties hypothesis of disease transmission (VanderWaal et al. 2016), a yearling's ability to link different social groups puts them at higher infection risk and their high network centrality enhances further transmission (Lloyd-Smith et al. 2005, Drewe 2010, Godfrey 2013). Thus, a high proportion of yearlings in the population could enhance the spread of communicable diseases. High centrality of yearlings can be explained by increased mobility of dispersing individuals, which are leaving natal groups at this age (Podgórski et al. 2014*b*). In a study on Belding's ground

Table 2. Variables explaining variation in individual centrality measures of the wild boar social network, based on data from Germany (2003–2004), Italy (2003–2004), and Poland (2008–2009). Sample size for all models is 77 individuals. We fit response variables with linear mixed-effects models with group identity and study area as random factors. Candidate explanatory variables included the continuous predictors group size, home range size (90% minimum convex polygon), spatial marginality (mean distance of individual home range centroid to all other home range centroids) and 2 factors: individual age and sex. The reference category for age was adult and reference for sex was male.

Response variable	Parameters	R^2_{marginal}[a]	$R^2_{\text{conditional}}$[b]	β	SE	P
Degree		0.26	0.94			
	Intercept			−0.34	0.52	0.527
	Age (yearling)			0.20	0.09	0.022
	Group size			0.10	0.05	0.062
	Spatial marginality			−0.0003	0.0001	0.039
Between-group degree		0.09	0.89			
	Intercept			0.48	0.10	<0.001
	Age (yearling)			0.04	0.02	0.037
	Group size			−0.02	0.01	0.057
	Spatial marginality			−0.00007	0.00003	0.023
Strength		0.79	0.99			
	Intercept			−4.83	0.40	<0.001
	Age (yearling)			0.11	0.04	0.006
	Group size			0.49	0.07	<0.001
	Spatial marginality			−0.0002	0.0001	0.127
Between-group strength		0.14	0.76			
	Intercept			−4.71	0.52	<0.001
	Age (yearling)			0.66	0.27	0.016
	Sex (female)			0.09	0.27	0.743
	Age × sex			−0.65	0.30	0.038
	Spatial marginality			−0.0004	0.0002	0.079
Closeness		0.82	0.99			
	Intercept			6.00	1.62	0.008
	Age (yearling)			0.51	0.18	0.007
	Group size			1.71	0.15	<0.001
	Spatial marginality			−0.0007	0.0004	0.089
Betweenness		0.06	0.06			
	Intercept			34.23	7.60	<0.001
	Sex (female)			−11.70	6.97	0.097
	Group size			−1.57	1.06	0.137

[a] Variance explained by fixed factors of the model, calculated according to Nakagawa and Schielzeth (2013).

[b] Variance explained by fixed and random factors of the model, calculated according to Nakagawa and Schielzeth (2013).

squirrels (*Urocitellus beldingi*), exploratory behavior of juvenile males contributed to increased connectivity of colonies, resulting in higher mean parasitic prevalence (VanderWaal et al. 2013). Similar processes could mediate the spread of many pathogens in wild boar populations. Finally, we detected spatial, social, and demographic effects on contact rates and structure when controlling for the variation across different study areas. Hence, these effects appear to be intrinsic to the species social system and should be considered in epidemiological modeling and management.

MANAGEMENT IMPLICATIONS

We found significant social structuring of contacts, with associations rates within groups 17-fold higher than among animals from different groups. Most of between-group associations occurred within 3 km and only sporadically beyond this distance. These social and spatial constraints on host contacts may reduce the rate of disease spread in the population, particularly for highly virulent and lethal pathogens, and result in rapid spread within groups with limited population-level effects. Management measures that reduce social and spatial constraints of wild boar contact rates, such as supplementary feeding (by creating contact hubs at the feeding sites) and intensive hunting (by inducing extensive movements and unnatural groupings) can potentially lead to increased disease transmission rates and should be avoided to mitigate epidemiological risks. In our study, yearling wild boar (<2 yr) showed exceptional connectivity within the population, highlighting their capacity for disease transmission. Thus, disease conscious management should consider targeted removal of yearlings to optimize disease control efforts.

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