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Do wild boar movements drive the spread of African Swine Fever?

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Abstract

The spatial behaviour of hosts can seriously affect the transmission of pathogens and spatial spread of diseases. Understanding the relationship between host movements and disease dynamics is of prime importance for optimizing disease control efforts. African swine fever (ASF), a devastating disease of wild and domestic suids, has been spreading continuously through eastern Europe since 2007. The wild boar (*Sus scrofa*) has been implicated in the epidemiology of this disease, but the role of wild boar movements in ASF dynamics and spread has not been studied and remains largely speculative. Here, we examined whether monthly parameters of wild boar movements (dispersal distance of yearlings, home range size of adult males and females) can explain variation in the spatio-temporal dynamics of the ASF outbreak in the wild boar population in north-eastern Poland, 2014–2015. We expected to observe a positive relationship between host mobility and disease spread. Contrary to our expectations, we found that movements of wild boar, despite their seasonal variation, were poor predictors of ASF dynamics in space and time. During the 2 years of the study, ASF spread gradually at a steady pace of 1.5 km/month without significant changes across seasons. None of the analysed movement parameters explained variation in the measures of ASF occurrence and spread (i.e., number of cases, prevalence, size and expansion rate of the outbreak area). We believe that the factor limiting the influence of host movements on ASF dynamics is the severity of the disease, which quickly hampers extensive movements and restricts disease transmission to only the most immediate individuals. Three natural factors constrain direct disease transmission: wild boar social structure, the short duration of low-level virus shedding and high virus-induced lethality, followed by indirect transmission through infected carcasses. These most likely shape the gradual spread of ASF in space and its persistence in already infected areas.

KEYWORDS
ASF, dispersal, home range, prevalence, spatial epidemiology

1 | INTRODUCTION

Movements of animal hosts can play a fundamental role in the transmission of pathogens and spatial dynamics of diseases. Hosts can contribute to disease spread through their spatial behaviour by moving away from the outbreak area and transmitting pathogens to susceptible individuals, leading to disease transmission between populations (Conner & Miller, 2004; Oyer, Mathews, & Skuldt, 2007). While long-distance animal migrations are particularly likely to facilitate the rapid spread of diseases (Altizer, Bartel, & Han, 2011), smaller scale variations in seasonal and cohort-specific movements can be responsible for pathogen transmission in nonmigratory species

(Cross et al., 2009). Increased home ranges and contact rates during the breeding period can enhance disease transmission between groups, while seasonal movements can contribute to disease spread across the landscape. The former has been implicated to play a role in the dynamics of Bovine tuberculosis in badgers (Carpenter et al., 2005; Rogers et al., 1998) and the latter in the spatial distribution of chronic wasting disease in mule deer (Conner & Miller, 2004). Movements of hosts are thus an integral part of disease dynamics, with the magnitude of the effect depending on host mobility and pathogen characteristics, such as transmission routes, infectiousness and lethality. Understanding the relationship between host movements and disease dynamics can help disease control actions to be optimized by allowing management efforts to be focussed on specific groups of individuals or seasons (Hirsch, Reynolds, Gehrt, & Craft, 2016; VanderWaal, Atwill, Hooper, Buckle, & McCowan, 2013).

African swine fever (ASF) is a contagious viral disease that affects wild and domestic suids (Costard, Mur, Lubroth, Sanchez-Vizcaino, & Pfeiffer, 2013). Most isolates of the ASF virus (ASFV) cause an acute or peracute haemorrhagic fever, with a lethality approaching 100% within approximately 8–20 days postinfection (Blome, Gabriel, & Beer, 2013). Animals can acquire the disease through direct contact with infected individuals, but the virus can persist in tissue and the environment for several weeks/months, and indirect transmission through fomites and contaminated meat may play an important role in disease dynamics (Costard et al., 2013; Wieland, Dhollander, Salman, & Koenen, 2011). Following its introduction to Portugal in 1957, ASF was present in Europe for several decades until it was eradicated from mainland Europe in 1995 (EFSA 2010). The current ASF epidemic started in 2007, with its emergence in Georgia and subsequent expansion across Armenia, Azerbaijan, Russian Federation, Belarus, Ukraine (Gogin, Gerasimov, Malogolovkin, & Kolbasov, 2013; Sánchez-Vizcaíno, Mur, Gomez-Villamandos, & Carrasco, 2015). It then entered the European Union in 2014 and has since been spreading across Estonia, Latvia, Lithuania, Poland (Sánchez-Vizcaíno et al., 2015; Śmietanka et al., 2016) and, most recently, Czechia (OIE 2017a) and Romania (OIE 2017b).

The wild boar (*Sus scrofa*) has been implicated in the spread and persistence of ASF in Europe. Until the recent past, it was believed that ASF fades out naturally in wild boar populations without spillover from domestic pigs or other sources of infection (Laddomada et al., 1994; Mur et al., 2012), but it has since become apparent that the disease can persist in wild boar populations alone (Oļševskis et al., 2016; Śmietanka et al., 2016). However, factors driving ASF dynamics in wild boar populations are poorly understood. In particular, the role of wild boar spatial behaviour in the epidemiology of ASF has not been systematically studied and remains largely speculative. Therefore, we urgently need to understand the influence of wild boar movements on ASF dynamics to better forecast and manage disease spread. This work is one of the first steps towards filling this knowledge gap.

The ecology and behaviour of the wild boar may facilitate ASF expansion due to the species' high mobility, sociality and abundance in Europe, which is now the highest ever recorded (Apollonio, Andersen, & Putman, 2010; Massei et al., 2015; Sáez-Royuela & Tellería, 1986). Wild boar social structure is centred around matrilineal social groups composed of a few subadult and adult females and their offspring (Gabor, Hellgren, Van den Bussche, & Silvy, 1999; Kaminski, Brandt, Baubet, & Baudoin, 2005; Podgórski, Scandura, & Jędrzejewska, 2014). The groups occupy home ranges of around 4–8 km^2 (Keuling, Stier, & Roth, 2008; Podgórski, Scandura et al., 2014), but wild boar exhibit remarkable intraspecific variation in spatial behaviour across a wide range of geographic locations and habitats (Boitani, Mattei, Nonis, & Corsi, 1994; Keuling, Stier, & Roth, 2009; Keuling et al., 2008; Podgórski et al., 2013). Within groups, the home ranges of individuals overlap extensively, whereas there is little overlap between groups; consequently, the frequency of direct contacts between individuals is much higher within than between groups (Pepin et al., 2016; Podgórski, Apollonio, & Keuling, 2018). Social groups may temporarily break, reform or exchange individuals (Gabor et al., 1999; Poteaux et al., 2009) but group members usually form stable and long-lasting relationships (Podgórski, Lusseau, Scandura, Sonnichsen, & Jędrzejewska, 2014). Thus, wild boar contact rates are to a large extent socially constrained, which could potentially restrict rapid spread of infectious diseases (Loehle, 1995).

Adult male and female wild boar occupy separate home ranges, the sizes of which may vary seasonally (Boitani et al., 1994). During the rutting season, which takes place in late autumn and early winter, the mobility of males increases. In this period, boars roam widely and regularly make excursions outside their home ranges in search of receptive females (Dardaillon, 1988; Graves, 1984; Spencer, Lapidge, Hampton, & Pluske, 2005). It is possible that these movements seasonally facilitate ASFV transmission between groups. Movements of pregnant females decrease around parturition but may increase several weeks postparturition due to intensive foraging during lactation (Morelle et al., 2015). Seasonal movements and home range shifts may also be driven by changes in weather conditions and resource availability (Keuling et al., 2009; Singer, Otto, Tipton, & Hable, 1981). Postweaning movements of young wild boar leaving their maternal groups are the main source of long-distance movements in populations. Dispersal most frequently occurs in the second year of life, when 40%–50% of yearlings leave their natal area (Keuling, Lauterbach, Stier, & Roth, 2010; Podgórski, Scandura et al., 2014; Truvé & Lemel, 2003). The majority of individuals disperse relatively short distances equal to 1–3 diameters of an average home range (<5 km), although longer dispersals (5–30 km) are also often observed (Keuling et al., 2010; Podgórski, Scandura et al., 2014; Prévot & Licoppe, 2013; Truvé & Lemel, 2003). Single individuals have been observed to cover distances of 50–250 km in a straight line (Andrzejewski & Jezierski, 1978; Jerina, Pokorny, & Stergar, 2014; Truvé & Lemel, 2003). These extensive movements could be a source of new infections in susceptible populations and contribute to ASFV spread. But how wild boar spatial behaviour affects ASF spread has not yet been evaluated.

Here, we used monthly parameters of wild boar movements to explain variation in the spatio-temporal dynamics of the ASF outbreak in north-eastern Poland. We expected to observe a positive relationship between host mobility and disease spread. In a specific manner, we hypothesized that larger yearling dispersal distances and home range sizes of male and female adult wild boar would lead to elevated transmission rates, resulting in a higher number of cases and prevalence, and an expansion of outbreak area.

2 | MATERIALS AND METHODS

2.1 | Study area

In 2014–2015, the ASF epidemic spread through the wild boar population in north-eastern Poland (Śmietanka et al., 2016). The first case was detected in February 2014, <1 km from the border with Belarus. By the end of 2015, the infected area stretched 120 km along and 34 km westwards from the border (Figure 1). This area is largely a field-woodland mosaic characterized by extensive agriculture and low human population density. The proportion of forest cover (31%) is higher than in the rest of the country, and there are several large forests of a few hundred square kilometres. The wild boar population is continuous throughout the area with densities at the start of the outbreak varying from 0.5 to 5 inds/km^2 (Regional Directorate of State Forests, Białystok, Poland). The wild boar movement data used in this paper originate from Białowieża Primeval Forest—a 600 km^2 forest complex located within the ASF infected area (Figure 1).

2.2 | Movement data

The parameters of wild boar movements used here were calculated using the telemetry locations of 58 animals collected from 2007 to 2011 in Białowieża Primeval Forest (Figure 1). A more detailed description of the trapping and tracking protocol can be found in Podgórski, Lusseau et al., 2014; Podgórski, Scandura et al., 2014. Using telemetry data, we calculated three parameters of wild boar movements to reflect variation in the spatial behaviour, and disease spreading capacity, of different sex and age classes. Young wild boar of both sexes disperse temporarily or permanently from maternal groups within the first 2 years of life (Podgórski, Scandura et al., 2014).Therefore, we estimated the monthly dispersal distance of yearlings (6–24 months old) as the average distance to the centre of the maternal home range. We used 1614 telemetry locations from 20 yearlings tracked on average for 9.5 months (190 individual-months in total) from 2007 to 2011. Maternity was established based on the analysis of genetic markers, and maternal home ranges were estimated from telemetry data (Podgórski, Scandura et al., 2014). Adult male and female wild boar occupy separate home ranges that may vary in size seasonally (Boitani et al., 1994). Therefore, we calculated monthly ranges (100% Minimum Convex Polygon—MCP) separately for adult (>24 months old) females (22 animals tracked on average for 5 months, in total 121 individual-months) and males (16 animals tracked on average for 4 months, in total 60 individual-months) using data collected from 2007 to 2010. For further analyses, data across all individuals and years in a given calendar month were averaged to give the mean value for each movement parameter per calendar month.

2.3 | Epidemiological data

Parameters of ASF dynamics were calculated using surveillance data routinely collected by the National Reference Laboratory for ASF at the National Veterinary Research Institute in Puławy, Poland. A detailed description of surveillance design and laboratory procedures can be found in Woźniakowski et al., 2015 and Śmietanka et al., 2016;. In this study, we used the results of diagnostic tests of 3,715 samples from dead or hunted wild boar collected from February 2014 to December 2015. The samples originated from three administrative units—Sokółka, Białystok and Hajnówka—where the ASF virus was circulating during the study period. In a more specific manner, we used surveillance data from risk zone III (ASF in both wild boar and domestic pigs) of Sokółka and Białystok counties and zone II (ASF in wild boar only) of Hajnówka county (Figure 1). All ASF cases recorded in 2014–15 in Poland occurred in these three areas. For a detailed description of risk zoning, see Śmietanka et al., 2016. We estimated four monthly parameters of ASF occurrence and spread to reflect the spatio-temporal dynamics of the disease: the (a) number of cases: the proportion of ASF cases detected in each of the 23 months of the study relative to the total number of ASF cases in wild boar detected during the whole study period, (b) prevalence: proportion of ASF positive samples relative to the number of samples tested within each month of the study, (c) size of outbreak area: the increase in size of the ASF infected area (calculated as the sum of circular areas of 2 km radius around each case) expressed as the difference between the size of the infected area in a given and previous month, (iv) spatial spread: rate of westward shift of the ASF frontline from the border with Belarus (location of the index case) expressed as the difference between the maximum distance of ASF cases to the border in a given and previous month.

2.4 | Statistical analysis

We analysed the relationship between wild boar movements and ASF spread using general mixed-effects models (Pinheiro & Bates, 2000). To this end, we constructed a database comprising four epidemiological parameters (i.e., response variables) calculated for each of the 23 months of disease outbreak and three parameters of wild boar movements (i.e., explanatory variables) in corresponding calendar months. We used the year of study as a random factor to control for interannual variation in disease dynamics. Explanatory variables expressed as proportions (number of cases and prevalence) were arcsin transformed prior to model fitting to improve normality and reduce skewness. Residuals of all fitted models were normally distributed as evidenced by visual inspection of the normal quantile plots of the residuals. We built two sets of models to account for potential delay in the observed effect of wild boar movements on ASF dynamics resulting from the time lag between an animal's death, field sampling and

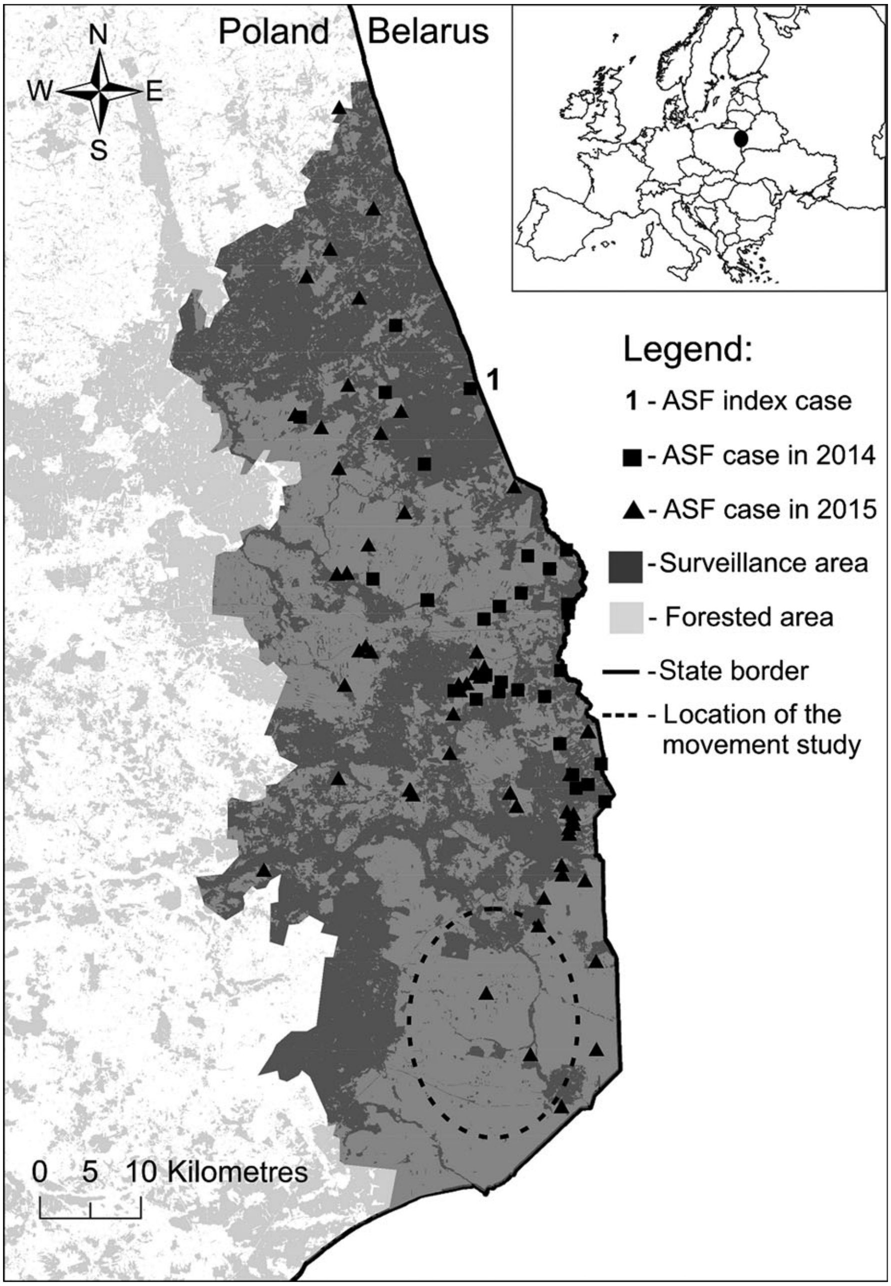

FIGURE 1 Location of the African swine fever (ASF) outbreak in the wild boar population in Poland, 2014–2015

laboratory testing. In the first set, we tested the effects of wild boar space use on epidemiological parameters in the same calendar month. In the second set, we tested the effects of wild boar space use on epidemiological parameters in the following calendar month. At last, we analysed the seasonality of ASF dynamics by constructing a third set of models with seasons (winter: December-February, spring: March-May, summer: June–August, autumn: September–November) as explanatory variables and the year of study as a random factor. We quantified the variation explained by the fixed effects of the models by calculating marginal R^2 (Nakagawa & Schielzeth, 2013) using MuMIn R-package (Bartoń, 2016). All statistical and spatial analyses were performed in R 3.3.2 (R Development Core Team 2015). Mixed models were computed using the “lme4” package (Bates, Maechler, Bolker, & Walker, 2015).

3 | RESULTS

3.1 | ASF epidemiological data

In total, 139 cases of ASF in wild boar were recorded in 2014 (57 cases) and 2015 (82 cases) in Poland (Supporting Information Table S1). The monthly number of cases averaged (±*SE*) 6.0 ± 1.1 (min.–max.: 0–18) and monthly prevalence averaged 5.6 ± 1.3% (min.–max.: 0–22) (Supporting Information Table S1). Seasonality of ASF occurrence was weak: The number of cases did not show significant seasonal changes (Table 1), but prevalence in spring (9.7 ± 3.8%) and summer (7.5 ± 2.9%) months tended to be higher than in autumn (1.6 ± 0.7%) and winter (3.2 ± 1.0%) (Table 1). The outbreak area increased in size at a rate of 30.7 ± 4.6 km^2 per month, reaching a total of 705.8 km^2 in December 2015 (Figure 2). The frontline of the outbreak, measured as the maximum westward distance between recorded ASF cases and the Belarusian border (Figure 1), advanced at a rate of 1.5 ± 1.3 km per month and expanded to 34.5 km away from the first case after 23 months of the outbreak. No seasonality was observed in the expansion rate of the outbreak area, as neither its increase in size nor rate of spread showed significant differences across seasons (Table 1). Instead, the outbreak area expanded rather steadily from the first occurrence of the disease (Figure 2).

3.2 | Effects of wild boar movements on ASF dynamics

Movements of wild boar showed remarkable variation across the year (Supporting Information Table S2). Monthly dispersal distances of yearlings ranged from 750 to 1815 m. Adult females varied the sizes of their monthly ranges fourfold over the year (from 0.3 to

TABLE 1 Coefficients of the models explaining the variation in four monthly variables of African swine fever (ASF) dynamics in the wild boar population in Poland, 2014–2015

		Coefficients of the predictors and their statistical significance		
Models of ASF dynamics	$R^2_{marginal}$ [a]	**Yearling dispersal**	**Adult female range**	**Adult male range**
Wild boar movements and ASF dynamics within a given month				
Number of cases	0.15	0.00005$^{n.s.}$	−0.154$^{n.s.}$	−0.003$^{n.s.}$
Prevalence	0.11	0.00001$^{n.s.}$	−0.161$^{n.s.}$	0.007$^{n.s.}$
Size of outbreak area	0.08	0.004$^{n.s.}$	−22.188$^{n.s.}$	0.377$^{n.s.}$
Spatial spread	0.18	0.009*	−7.328$^{n.s.}$	−0.831$^{n.s.}$
Wild boar movements and ASF dynamics in the following month				
Number of cases	0.07	−0.00002$^{n.s.}$	0.006$^{n.s.}$	0.006$^{n.s.}$
Prevalence	0.04	−0.00004$^{n.s.}$	0.021$^{n.s.}$	0.032$^{n.s.}$
Size of outbreak area	0.09	0.002$^{n.s.}$	−9.287$^{n.s.}$	6.372$^{n.s.}$
Spatial spread	0.05	0.001$^{n.s.}$	2.199$^{n.s.}$	−1.210$^{n.s.}$
Seasonality[b]		**Winter**	**Spring**	**Summer**
Number of cases	0.11	0.048$^{n.s.}$	0.058$^{n.s.}$	0.092$^{n.s.}$
Prevalence	0.21	0.064$^{n.s.}$	0.145*	0.147*
Size of outbreak area	0.12	14.022$^{n.s.}$	14.729$^{n.s}$	19.048$^{n.s.}$
Spatial spread	0.14	3.333$^{n.s.}$	−1.267$^{n.s.}$	−3.300$^{n.s.}$

Note. *$0.05 < p < 0.1$. [a]Variance explained by fixed factors of the model, calculated according to Nakagawa & Schielzeth, 2013. [b]Coefficients for factors shown in contrast to the reference level—autumn.
$^{n.s.}$not significant ($p > 0.1$).

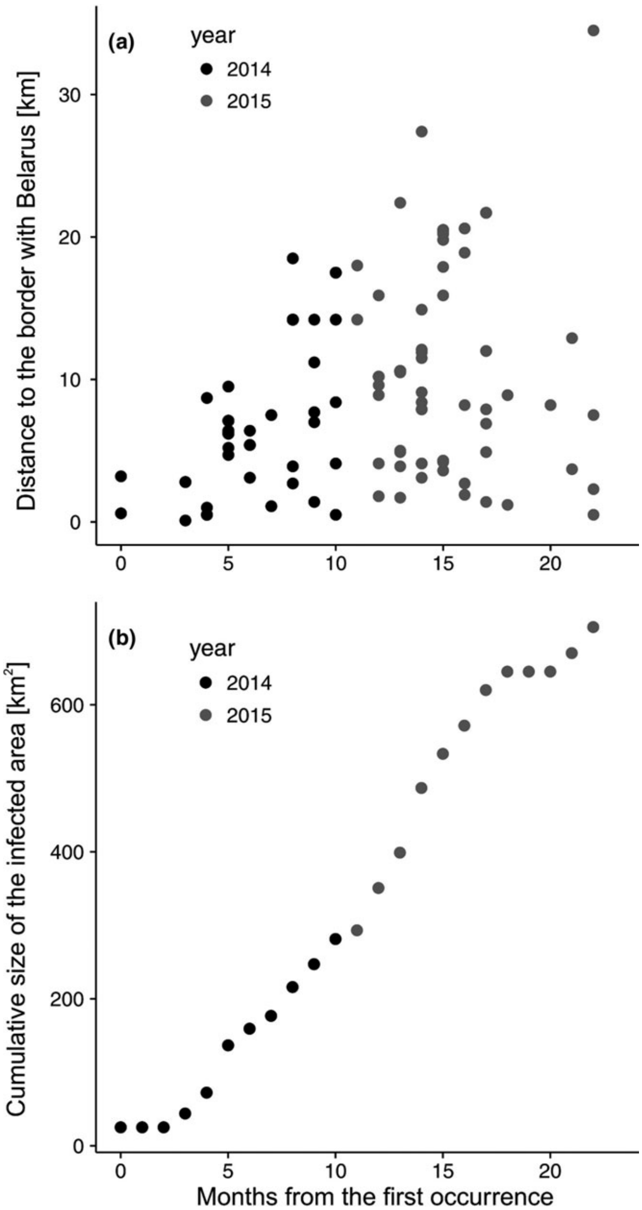

FIGURE 2 Spatial spread of African swine fever (ASF) in the wild boar population in Poland (2014–2015) represented by the (a) increasing distance of ASF cases to the border with Belarus, where the index case was found and (b) growing size of the outbreak area

1.4 km^2), while adult males by an order of magnitude (from 0.1 to 2.1 km^2). Despite this variation in wild boar movements, we found no evidence that the spatial behaviours of any of the sex and age classes significantly influenced the spread of ASF (Table 1, Figure 3, Supporting Information Figure S1). None of our predictors explained the variation in the monthly numbers of cases, prevalences, sizes of the outbreak area or its spatial spread when movement data were used to explain the epidemiological parameters in the matching calendar month as well as when the epidemiological data from the following month were considered (Table 1). There was a marginally significant ($p = 0.07$) effect of dispersal distance on the spatial spread of ASF (Table.1, Figure 3).

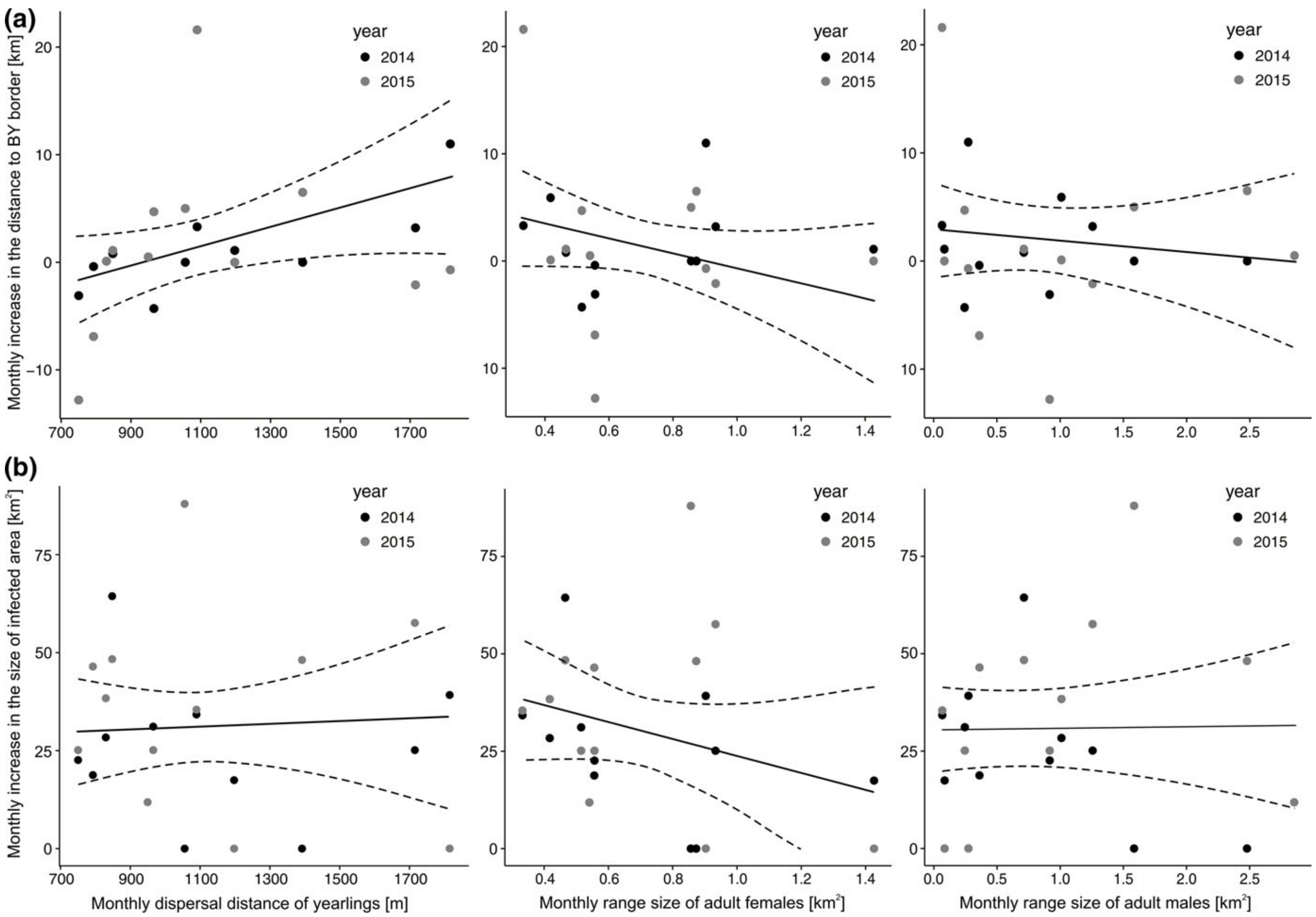

FIGURE 3 Effects of wild boar movements on the spatial spread of the African swine fever (ASF) outbreak. None of the three movement parameters explained the variation in monthly advance of the outbreak frontline (a) and outbreak area size (b) (Table 1). Solid lines correspond to the effect estimates obtained with mixed-effects models and broken lines represent 95% confidence intervals around the estimate

4 | DISCUSSION

During the first 2 years of ASF occurrence in the wild boar population in Poland, the disease spread gradually in space and time, contrary to the early predictions that forecasted a rapidly progressing outbreak. The frontline of the outbreak advanced at a steady pace of 1.5 km/month, without significant changes across the seasons. This disease spread rate corresponds to the range of wild boar movements at a monthly scale (Supporting Information Table S2) and is within the range at which within- and between-group contacts occur (Podgórski et al., 2018). The frequency of ASF detections we report (on average 6 per month) provides enough intermonthly variation to be compared with movement data at the same temporal scale. We thus believe that spatial and temporal scales of epidemiological parameters and host movements match each other and can be used to draw meaningful inferences on the relationship between these two data sets. Despite the frontline of the ASF outbreak steadily shifting away from the Belarusian border, new cases were still repeatedly recorded in close proximity to the border throughout the 23 months of study (Figure 2). This suggests a continuous influx of infected individuals from Belarus, which is supported by genetic analysis of ASFV phylogeny (Śmietanka et al., 2016) and localized endemicity. During the study period, only three independent outbreaks in domestic pigs occurred in the study area. They originated from the wild boar population and epidemiological investigations showed no evidence of spillover from domestic pigs to wild boar. Thus, we believe that the patterns of ASF spread observed in this study represent a natural process in a medium to high density wild boar population with limited human-mediated transmission. In other ASF-affected areas with greater contribution of human-mediated transmission, rates of ASF spread are likely to be higher (EFSA 2017).

Contrary to our expectations, we found that the movements of wild boar were poor predictors of ASF dynamics in space and time. None of the analysed movement parameters explained the variation in the measures of ASF occurrence and spread. There could be several reasons for why this effect was not observed. First, increased movements do not necessarily translate into the higher contact rates between individuals required for direct disease transmission. Seasonal movements in wild boar are usually driven by a pursuit of habitats offering better foraging opportunities or shelter (Keuling et al., 2009; Singer et al., 1981) and may not result in increased mixing of individuals. Furthermore, contact rates among individuals are strongly socially structured, that is within-group contacts are by an order of magnitude more frequent than those between-groups (Pepin et al., 2016; Podgórski et al., 2018). This could represent a solid social barrier to pathogen transmission (Loehle, 1995) and may particularly constrain outbreaks of highly virulent diseases, which will spread rapidly within groups but slowly between them (Altizer et al., 2003; Cross, Lloyd-Smith, Johnson, & Getz, 2005). Increased movements of adult males during the breeding season (Spencer et al., 2005) could potentially facilitate disease transmission between groups, but we found this to not be the case at the population level in our study. The severe physiological effects of rapidly progressing ASF probably hamper the breeding pursuits of infected males and thus make transmission of the disease by this class of individuals very rare. Second, contact rates between live individuals (sick and susceptible) may not be of paramount importance for maintaining the transmission chain. In an experiment with pigs, the amount of the Georgia/2007-like ASF viruses in excretions was 2–4 times lower than the viral load in blood (Guinat et al., 2016), and a similar pattern can be expected for wild boars.

A third, and perhaps the most important, factor limiting the influence of host movements on ASF dynamics is the severity of the disease. The ASFV strain currently circulating in Eastern European countries is highly virulent, causing 90%–100% lethality within 10–20 days postinfection (Blome, Gabriel, Dietze, Breithaupt, & Beer, 2012; Blome et al., 2013; Gallardo et al., 2017). The clinical picture corresponds to an acute form of ASF (Blome et al., 2013), characterized by a short incubation period of 4 days followed by severe symptoms including impaired mobility, digestion disorders and laboured breathing (Gallardo et al., 2017). Thus, infected animals have a very short time window (<1 week) to move about and shed the virus before the disease symptoms seriously hamper any extensive movements and restrict disease transmission by live hosts to the most immediate individuals, that is members of the same social group. Therefore, indirect transmission through contacts with infected carcasses seems to play an important role in ASF epidemiology (EFSA 2015, Guinat et al., 2016; Lange & Thulke, 2017). ASFV remains stable and infectious in the tissues of infected animals for extended periods of time, from several weeks to months depending on the weather conditions (Costard et al., 2013). Hence, the availability of infectious carcasses and frequency at which these are encountered by susceptible animals will likely contribute to the long-term disease persistence in an area. Although encounter rates between live and dead wild boar do not seem high (Lange & Thulke, 2017; Probst, Globig, Knoll, Conraths, & Depner, 2017; Selva, Jędrzejewska, Jędrzejewski, & Wajrak, 2005), lengthy decomposition of carcasses combined with contamination of the environment with the virus may pose a substantial and prolonged risk of generating new infections.

Overall, our results indicate that wild boar movements only play a minor role in ASF dynamics at the monthly scale and point to the importance of other factors implicated in the epidemiology of ASF. We believe that three natural factors constrain direct disease transmission: (a) wild boar social structure, (b) the short duration of low concentration virus shedding by sick animals through oral and rectal excretions and (c) the high lethality of the virus combined with indirect transmission through infected carcasses. These shape the spatio-temporal pattern of gradual ASF spread and its persistence in already infected areas, as observed in this study. We note that the spatial behaviour of wild boar could still influence ASF transmission at finer spatio-temporal scales (e.g., daily movements), enhancing local spread of the disease. At last, we cannot completely rule out the role of human activities in the spread of ASF in the area. ASFV can persist in the environment and spread via fomites, such as contaminated clothes and equipment (Costard et al., 2013; Mur et al., 2014). Although there was no evidence of spillover from domestic pigs or other human-induced spread in the area, poor biosecurity during hunting could enhance local spread of ASFV in the wild boar population. Yet, the relative contributions to ASF dynamics of various risk factors related to both wild boar and human behaviour require further study.

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CONFLICT OF INTERESTS

Authors declare no conflict of interest.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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