International Journal for Parasitology: Parasites and Wildlife 17 (2022) 257–262

Contents lists available at ScienceDirect

International Journal for Parasitology: Parasites and Wildlife

journal homepage: www.elsevier.com/locate/ijppaw

Predicting the risk of *Alaria alata* infestation in wild boar on the basis of environmental factors

Daniel Klich[a], Marek Nowicki[b,*], Anna Didkowska[b], Zbigniew Bełkot[c], Bartłomiej Popczyk[a], Jan Wiśniewski[b], Krzysztof Anusz[b]

[a] *Department of Animal Genetics and Conservation, Institute of Animal Science, Warsaw University of Life Sciences, Ciszewskiego 8, 02-786, Warsaw, Poland*
[b] *Department of Food Hygiene and Public Health Protection, Institute of Veterinary Medicine, Warsaw University of Life Sciences, Nowoursynowska 159, 02-776, Warsaw, Poland*
[c] *Department of Food Hygiene of Animal Origin, Faculty of Veterinary Medicine, University of Life Sciences in Lublin, Akademicka 12, 20-950, Lublin, Poland*

ARTICLE INFO

Keywords:
Alaria alata
Wild boar
Red fox
Raccoon dog
Wetlands

ABSTRACT

Alaria alata is an emerging parasite that poses a potential risk for those consuming game, pork, snails and frogs. One paratenic host of *A. alata* that is known to play an important role in its spread through its feeding habitats is the wild boar. However, no statistical analysis of the influence of aquatic environments and carnivores on the occurrence of *A. alata* in wild boars has yet been performed. The present study combines a small-scale analysis based on hunting districts in the Mazowieckie province with a large-scale analysis based on data for all provinces in Poland. We applied various modeling approaches, including logistic regression and a generalized linear model in order to determine the presence, intensity and prevalence of *A. alata.* We used the *Alaria* mesocercariae migration technique (AMT) to estimate the risk of *A. alata* among wild boar in a given hunting district or province. The small-scale analysis found that mesopredators (red fox (*Vulpes vulpes*)) and racoon dog (*Nyctereutes procyinoides*) were likely to influence *A. alata* infestation of wild boar; however, the effect was weak, probably as a result of the large home range size of these animals. The large-scale analysis found that wetlands influence the prevalence of *A. alata* in wild boar, with the estimated risk increasing in the north of the country; this finding is consistent with other studies. Our findings indicate that the occurrence of *A. alata* in wild boar requires analysis on many levels, and environmental factors play a key role in risk assessment.

1. Introduction

Even though with the possibility is very low, *Alaria alata,* a widespread emerging parasite, may pose a potential risk for human consumers of game, pork, snails and frogs (Möhl et al., 2009; Korpysa-Dzirba et al., 2021). The life cycle of this parasite is complex and includes definitive, intermediate and paratenic hosts. The definitive hosts are carnivores such as canids, felids and mustelids (Wójcik et al., 2001; Takeuchi-Storm et al., 2015). In Europe, the definitive hosts are typically red foxes (*Vulpes vulpes*), wolves (*Canis lupus*) and racoon dogs (*Nyctereutes procyinoides*) (Murphy et al., 2012; Rentería-Solís et al., 2013; Ozoliņa et al., 2018).

The *A. alaria* fluke produces its eggs (a dispersive parasite form) in the digestive system of the definitive host, and they are then excreted into the environment with the feces. These are consumed by intermediate hosts such as snails, tadpoles and frogs, where they develop into miracidia (Portier et al., 2012; Patrelle et al., 2015; Voelkel et al., 2019; Ozoliņa et al., 2021). In the paratenic host, the parasite does not reach the adult stage, but it can survive for months in the muscle or adipose tissue (Riehn et al., 2013). The parasite can later reinfect the definitive host if the paratenic host is consumed. Several mammal species have been described as paratenic hosts (Shimalov and Shimalov, 2001; Rentería-Solís et al., 2018); of these, the wild boar (*Sus scrofa*) is known to play an important role in spreading *A. alata* due to its feeding habitats (Ozoliņa et al., 2020).

In the context of public health, it must be noted that *A. alata* poses a potential risk to consumers of wild boar meat. Alariosis has been described in humans (McDonald et al., 1994; Kramer et al., 1996); however, the etiological agent in this case was *Alaria americana*, and not *A. alata*, which occurs in Europe. Considering the close relationships between these two *Alaria* species and the difficulties in the diagnosis of alariosis in humans (non-specific symptoms), it should be assumed that

* Corresponding author.
E-mail address: marek_nowicki@sggw.edu.pl (M. Nowicki).

https://doi.org/10.1016/j.ijppaw.2022.03.004
Received 13 January 2022; Received in revised form 2 March 2022; Accepted 3 March 2022
Available online 10 March 2022

A. alata may also be a potential zoonotic agent in Europe, as classified by organizations such as the Swiss Agency for the Environment, Forests and Landscape. In such cases, humans may act as paratenic hosts.

As eating frogs is a rather local dietary habit, the most likely route of transmission to humans in Europe is the consumption of infected wild boar meat (Dollfus and Chabaud, 1953). In Europe, the prevalence of *A. alata* in wild boar is thought to range from 0.6% (France, magnetic stirrer method) (Porteir et al., 2011) to as much as 44.3% (northeast Poland, mesocercariae migration technique) (Strokowska et al., 2020). *A. alata* larvae are believed to be capable of effective survival in a refrigerator; therefore, as noted by the French Agency for Food, there is a real risk of human infection as a result of eating meat from *A. alata*-infected wild boar (Korypsa-Dzirba et al., 2021). The most effective method of avoiding infection would appear to be proper heat treatment, as is the case with *Trichinella* spp. (Gamble et al., 2019). However, considering the popularity of homemade semi-raw meat products, *A. alata* should not be neglected as a potential pathogen for humans.

The infection rate among wild boar depends on their exposure to the sources of *A. alata*. Previous studies have reported it to be correlated with the number of foxes (definitive host) living in the same territory (Möhl et al., 2009) and the presence of amphibians in the area (Ozoliņa et al., 2021). The presence of amphibians can be estimated indirectly based on the occurrence of marshland and water areas in a given region. Previous studies have noted a significant difference in the occurrence of *A. alata* in snails and frogs between seasons: a prevalence of 30% has been observed among snails and frogs in the autumn, and 100% in the spring (Wójcik et al., 2001).

However, no direct evaluation has been performed of the influence of local aquatic environments and carnivores on the occurrence of *A. alata* in wild boars in a given area. Such data would be of great importance in identifying areas where monitoring should be increased; it could also be used to outline further research directions and support effective preventive activities. Therefore, the aim of the present manuscript was to determine the influence of environmental factors in predicting the occurrence of *A. alata* infestation in wild boar.

2. Material and methods

2.1. Sample collection and examination

Samples were collected from 576 hunted wild boar from 14 of the 16 Polish Provinces. Provinces (called also voivodeships) are the highest-level administrative division in Poland. The exact numbers of samples taken from individual provinces are presented in Table 1. The procedure used to collect and transport material is described by Strokowska et al. (2020). Samples of muscles, adipose and connective tissue were tested with the *Alaria* mesocercariae migration technique (AMT) according to Riehn et al. (2010). The characteristic movement and morphological features of this parasite (the body is clearly divided into two sections, with a wing-like shape at the front) were used to assess its presence in tissues. All samples were tested within a maximum of seven days after material collection.

Table 1
Source of data and number of samples for each province included in the analysis.

Province	Present study data	Bilska-Zając et al. (2021)	Strokowska et al. (2021a)	total
Dolnośląskie	10	108		118
Kujawsko-Pomorskie	33			33
Lubelskie	81	7	500	588
Lubuskie		21		21
Łódzkie	19	19		38
Małopolskie	3	3,126		3,129
Mazowieckie	243	1		244
Opolskie		11		11
Podkarpackie	13	30		43
Podlaskie	12			12
Pomorskie	24	2		26
Śląskie	2	58		60
Świętokrzyskie	2	179		181
Warmińsko-Mazurskie	130			130
Wielkopolskie	2	17		19
Zachodniopomorskie	2	5		7
TOTAL	576	3,584	500	4,660

2.2. Data elaboration and statistics

2.2.1. Small-scale analysis

Samples with known locations, i.e., where these wild boars were hunted, were assigned to hunting districts. To determine the small-scale impact of variables on wild boar infestation with *A. alata*, only samples from hunting districts in the Mazowieckie province were examined. The numbers of the most common mesopredators, namely the red fox (*Vulpes vulpes*) and raccoon dog (*Nyctereutes procyonoides*), were obtained from the Polish Hunting Association for each of the hunting districts. This data was obtained for 2017. The density of predators in each hunting district was then calculated based on its area.

For each hunting district, land cover data was also obtained from the Corine Land Cover database (CLC) for 2018 (https://land.copernicus.eu). The type of land cover was determined using Quantum GIS (version 3.4.5), which is open source geographic information system (GIS) software. All cover types within the boundaries of each hunting district were calculated with regard to their percentage. Following this, four cover types were selected for further analysis: areas covered by water (referred to with codes 5.1.1 and 5.1.2 in CLC), wetlands (referred to with code 4.1.1 in CLC), arable land (referred to with code 211 in CLC) and forests of various types (referred to with codes 3.1.1, 3.1.2, and 3.1.3 in CLC). Of these, the first two (areas covered by water and wetlands) were expected to have an impact on *A. alata* infection, while the last two cover types (arable and forests) dominated in the hunting districts.

The impact of environmental characteristics on the occurrence of *A. alata* mesocercariae in wild boars was determined using a logistic regression model which included all six known explanatory variables for the hunting districts as covariates: density of red foxes as number of individuals per 10,000 km^2 (FOX); density of raccoon dogs as number of individuals per 10,000 km^2 (RACOON); percentage of areas covered by water (WATER); percentage of wetlands (WETLANDS); percentage of arable land (ARABLE); percentage of forested areas (FORESTS). All *A. alata*-infected samples were marked as 1; all negative samples were marked as 0. The explanatory variables were verified based on Pearson's correlation coefficient: all values were lower than $|r| = 0.7$. The quality of the model was verified according to the percentage of correctly classified cases and AUC (area under the ROC curve).

The impact of similar environmental characteristics on the intensity of *A. alata* mesocercariae in wild boar was evaluated using a generalized linear model with gamma distribution and the log link function. In this model, the dependent variables were the number of *A. alata* mesocercarie in wild boar (only infected cases); the explanatory variables were (FOX), (RACOON), (WATER), (WETLANDS), and (FORESTS). The variable for arable land (ARABLE) was not included because it was closely correlated with FORESTS (Pearson's $r = -0.809$, $p = 0.000$). Model selection was performed according to Burnham and Anderson (2002), where the model presenting the lowest AIC value was chosen as the best one. Akaike weights (ω_i) were calculated for each model, and the sum of Akaike weights ($\sum\omega_i$) for each variable included in the models was within $\Delta AIC = 2$.

2.2.2. Large-scale analysis

The prevalence of *A. alata* was evaluated against land cover types and red fox density for all provinces. Raccoon dog density was not included due to lack of data. The prevalence of *A. alata* in wild boar in a given province was estimated based on data from this study and recent literature data (Table 1). All sources employed similar methods of *A. alata* detection (Strokowska et al., 2021b), which allowed us to increase the number of samples in a given province and minimize bias due to low sample size. In total, the prevalence *A. alata* was determined based on three sources, with the final prevalence being calculated as a weighted mean of these sources, based on the number of studied samples. The number of samples used and the sources of data are presented in Table 1. The selected cover types of each province were also determined with regard to the four cover-type percentages outlined above, in a similar way as for the small-scale analysis (for hunting districts). A generalized linear model was used with Tweedie distribution and the identity link function, which presented the best values for overdispersion. Model selection (similar to small-scale analysis for infected cases) was performed according to Burnham and Anderson (2002) using the following explanatory variables: (FOX), (WATER), (WETLANDS), and (FORESTS). RACOON was omitted from the analysis due to a lack of data on raccoon dog density in the provinces for 2017. In addition, ARABLE was omitted because it was highly correlated with FORESTS (Pearson's $r = -0.748$, $p = 0.001$). All models were verified (including the null model) with regard to the AICc value (for small sample size); again, the model that presented the lowest AICc value was chosen as the best one. Akaike weights (ω_i) were calculated for each model, and the sum of Akaike weights ($\sum\omega_i$) for each variable included in the models were within 95% confidence intervals ($\sum\omega i = 0.95$).

The risk of *A. alata* prevalence in wild boar was also estimated for given provinces in Poland. The prevalence was compared on the basis of the data from the present study, as well as literature values and the prevalence predicted by the model. When predicting the prevalence, only WETLANDS values that significantly explain the prevalence of *A. alata* in provinces were used. It was also assumed that the prevalence could not exceed 100%; where the predicted prevalence was higher, the value was lowered to 100%.

3. Results

3.1. Small-scale analysis

The occurrence of *A. alata* mesocrecarie in wild boar was significantly predicted only by raccoon dog density (RACOON) in each hunting district (Table 2). All other explanatory variables were statistically insignificant ($P > 0.05$). The B coefficient of RACOON was positive, indicating that the probability of *A. alata* mesocercarie in wild boar increases at higher raccoon dog densities. The model, however, had weak parameters: only 73% of all cases were correctly classified, and the AUC value was 0.614, indicating the model had low accuracy.

The highest-ranked generalized linear model of intensity of *A. alata* in wild boar was statistically significant ($\chi2 = 5.144$, df = 1, p = 0.023) and included only FOX (Table 3). All other variables (RACOON, WATER, WETLANDS and FORESTS) were excluded during the selection procedure. Nevertheless, the difference in the explanatory power of the given variables was low because six models were included within the $\Delta AIC = 2$ of the highest-ranked models, and the ΔAIC equaled 0.51 between the highest-ranked model and the next-highest-ranked model (with FOX and RACOON included). Moreover, the ΔAIC between the highest-ranked model and the null model equaled only 3.14 (Table 4). FOX was present in all models within $\Delta AIC = 2$, thus its sum of Akaike weights was the highest ($\sum\omega_i = 0.5$); RACOON and WETLANDS also demonstrated high Akaike weight sums ($\sum\omega_i = 0.18$ and ($\sum\omega_i = 0.12$).

Table 2
The effect of FOX, RACOON, FORESTS, ARABLE, WATER and WETLANDS on the probability of occurrence of *A. alata* mesocercariae in wild boar in the logistic regression model (*B* – beta coefficient, *SE* – standard error, *OR* – odds ratio, N = 196).

Source	*B*	*SE*	*Wald* X^2	*P*	*OR*
Intercept	−0.333	1.107	4.439	0.035	0.097
FOX	−0.023	0.020	1.133	0.249	0.997
RACOON	0.328	0.157	4.369	0.037	1.388
FORESTS	1.816	1.546	1.379	0.240	6.144
ARABLE	1.872	1.417	1.744	0.187	6.500
WATER	−4.855	9.722	0.249	0.617	0.008
WETLANDS	−70.818	74.034	0.915	0.339	0.000

Table 3
The effect of FOX on the number of *A. alata* mesocercariae in wild boar in the highest-ranked generalized linear model (B – beta coefficient, SE – standard error, CI – confidence intervals, N = 53).

Source	*B*	*SE*	*Wald* X^2	*P*	*Lower CI*	*Upper CI*
Intercept	2.063	0.202	114.157	0.000	1.766	2.560
FOX	0.034	0.016	4.505	0.034	0.003	0.065

3.2. Large-scale analysis

The highest-ranked generalized linear model for the prevalence of *A. alata* in wild boar was statistically significant ($\chi2 = 10.363$, df = 1, p = 0.001) and included only WETLANDS (Table 5). The model presented a clearly higher Akaike weight ($\omega_i = 0.57$) than the other lower-ranked models (Table 6) and differed from the null model by AICc = 7.29. The estimated prevalence of *A. alata* increased with the percentage of wetland cover in provinces; however, the model predicted a prevalence of over 100% for the Podlaskie province (Fig. 1).

The calculated trends of *A. alata* prevalence in Poland as a whole were similar to the predicted values; however, differences can be observed in particular provinces. On the basis of literature values and data from the present study, our calculations indicated an increase in the prevalence of *A. alata* in wild boar in the north and north-east (Fig. 2A). These values ranged from 0% in Opolskie in the south-west to 54.6% in Warmińsko-Mazurskie in the north-east, but higher values were also observed in the Zachodniopomorskie (in the north-west, 42.9%) and Podlaskie (north-east, 41.7%) provinces.

Our model did predict a higher prevalence of *A. alata* in the north (Fig. 2B), with values ranging from 6.8% in Małopolskie, 7.5–7.7% for Śląskie and Opolskie Provinces in the south, to over 100% in Podlaskie in the northeast. Higher values were also observed in the Warmińsko-Mazurskie (43.3%) and Kujawsko-Pomorskie (30.7%) provinces.

4. Discussion

As predicted, areas covered with wetlands appear to be of significant importance in determining the occurrence of *A. alata* in wild boar. Our findings also indicate that mesocarnivore density also had an important influence on *A. alata* occurrence and intensity in wild boar. While the land cover types showed an effect in the large-scale analysis, mesocarnivores demonstrated a weak effect in the small-scale analysis, i.e., in hunting districts. Although our findings are generally in line with current knowledge, some effects seem to derive from more complex

Table 4
Ranking of the models (including the null model) predicting the number of *A. alata* in wild boar within ΔAIC=2 (ΔAIC – AIC differences, ω_i – Akaike weights; Rank – rank of the models based on AIC values). Variables: see methods. Best model in bold.

Model	*ΔAIC*	ω_i	*Rank*
FOX	**0.00**	**0.15**	**1**
FOX + RACOON	0.51	0.11	2
FOX + RACOON + WETLANDS	1.58	0.07	3
FOX + WATER	1.83	0.06	4
FOX + FOREST	1.83	0.06	5
FOX + WETLANDS	1.97	0.06	6
Null	3.14	0.03	10

Table 5
The effect of WETLANDS on the prevalence of *A. alata* mesocercariae in wild boar in the highest-ranked generalized linear model (B – beta coefficient, SE – standard error, CI – confidence intervals, N = 53).

Source	*B*	*SE*	*Wald* X^2	*P*	*Lower CI*	*Upper CI*
Intercept	5.817	3.586	2.631	0.105	−1.212	12.846
WETLANDS	5,445.837	1,958.886	7.729	0.005	1,606.492	9,285.182

Table 6
Ranking of the models (including the null model) predicting the prevalence of *A. alata* in wild boars in provinces within 95% confidence intervals ($\sum \omega i = 0.95$) (ΔAIC – AIC differences, ω_i – Akaike weights; Rank – rank of the models based on AIC values). Variables: see methods. Best model in bold.

Model	*ΔAICc*	ω_i	*Rank*
WETLANDS	**0.00**	**0.57**	**1**
WETLANDS + FOREST	2.98	0.13	2
WETLANDS + FOX	3.34	0.11	3
WETLANDS + WATER	3.64	0.09	4
WETLANDS + WATER + FOREST	7.09	0.02	5
WETLANDS + FOX + FOREST	7.18	0.02	6
Null	7.29	0.01	7
WATER	7.34	0.01	8

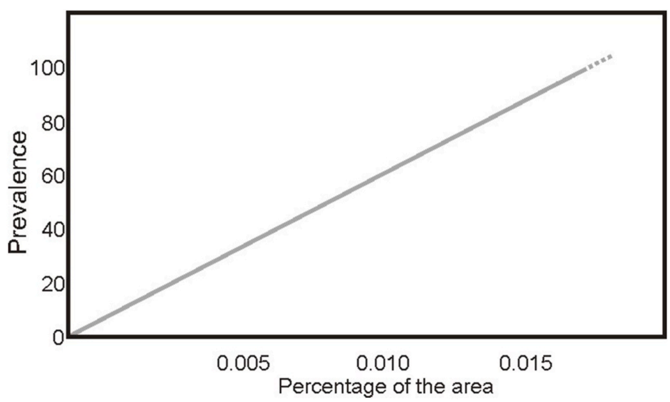

Fig. 1. The trend in prevalence of *A. alata* in provinces with WETLANDS.

relations.

It is not surprising that wetlands have an effect on the prevalence of *A. alata* in wild boar as the life cycle of *A. alata* requires an aquatic environment: miracidia, an invasive form of *A. alata,* are released from eggs into water, thus the first intermediate hosts are freshwater animals (Möhl et al., 2009). It has previously been proven that an abundance of wetlands is positively correlated with the occurrence of adult forms of this parasite in final hosts (Ramisz and Balicka-Ramisz, 2001). This tendency was also confirmed by Tylkowska et al. (2018) in Poland, where the most foxes that were found to be infected with *A. alaria* were those living near water reservoirs.

Regarding the presence of *A. alata* mesocercariae in wild boar, Sailer et al. (2012) reported a higher prevalence in an area of Austria that is located in the backwaters of two rivers than an area to the north of one of these rivers, i.e. with less wetland, as described previously by Pestál (1989). Therefore, the lack of this water-related effect in the present study is puzzling. Although this may seem of minor importance, some regions of Poland, especially the northern part, are characterized by large numbers of lakes and of water resources in general (Górniak and Piekarski, 2002). This could partially correlate with WETLANDS and cause a lack of effect by areas covered by water.

Our present findings do not suggest that wetlands or other cover types demonstrated any effects in the small-scale analysis. This may, on the one hand, result from the rough scale of Corine Land Cover, but it might also be caused by the home range size of animals. The mean area of the studied hunting districts was 5,000 ha, which is generally larger than that of the home range of wild boar, which typically cover several hundred hectares (Sodeikat and Pohlmeyer, 2002). However, this home range is dependent on many factors: for example, males and young individuals may have larger home ranges of over 1,000 ha (Mauget, 1980; Keuling et al., 2008). Home range size is also strongly influenced by aspects of landscape structure, such as the number of forest patches or the degree of elevation (Fattebert et al., 2017). In addition, the home range can extend to 3,500 ha under the influence of hunting (Sodeikat and Pohlmeyer, 2002); this effect could also be strengthened by the dispersion of animals as a result of hunting pressure (Keuling et al., 2008). Furthermore, the wild boar has a large dispersive ability, and individuals can migrate up to several hundred kilometers (Keuling et al., 2010; Jerina et al., 2014). This is an important consideration as, during the sampling period, wild boar were under increased hunting pressure

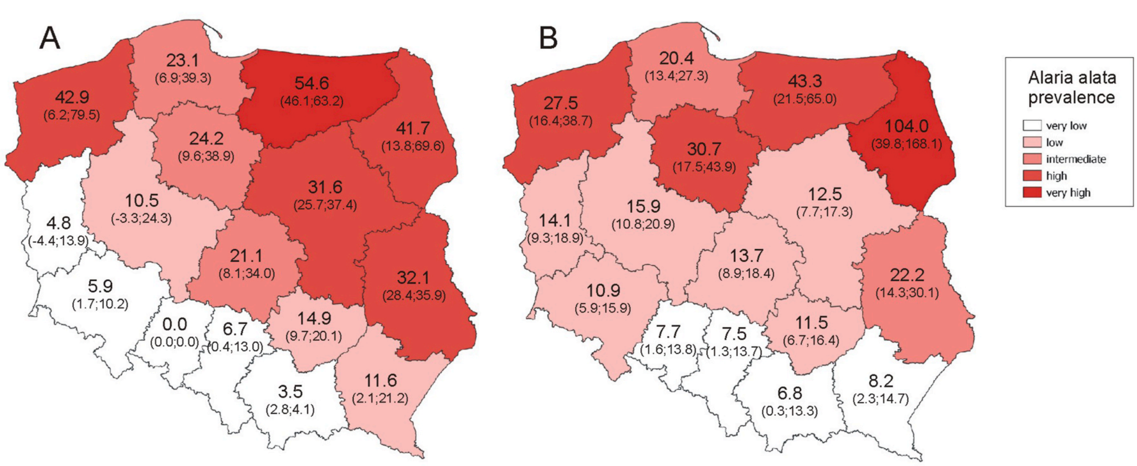

Fig. 2. The prevalence of *A. alata* in wild boar in provinces in Poland calculated from literature values and data from the present study (A) and predicted by percentage of areas covered by WETLANDS (B) (for detailed information, see: Methods). The figure shows prevalence values for a given province and confidence intervals (lower; upper).

aimed at slowing the spread of African swine fever (Klich et al., 2021). Therefore, it would be reasonable to assume that the home range size of wild boar in Poland was significantly larger during the year of sample collection, and the lack of effect that was observed in the small-scale analysis would not be present in other hunting conditions.

In addition to the land cover effect, mesopredators seem to play a significant role in increasing the intensity of *A. alata* in wild boar. This was noted in the small-scale analysis, in which, despite having somewhat low explanatory power, red fox and raccoon dog numbers were shown to have an effect. These species are present as definitive hosts in the *A. alata* cycle (Takeuchi-Storm et al., 2015; Korpysa-Dzirba et al., 2021), and the red fox is considered to be the main definitive host of *A. alaria* in Europe (Portier et al., 2011). Indeed, a recent study in Poland found a high prevalence of *A. alata* in red foxes (78.7%) based on intestinal examination (Karamon et al., 2020). *A. alata* does not yet appear have been described in raccoon dogs in Poland; however, it has been confirmed in neighboring Lithuania, and the data suggests that *A. alata* may even be found in greater abundances in raccoon dogs than in red foxes (Bružinskaitė-Schmidhalter et al., 2012). As such, it might be recommended to test raccoon dogs in Poland for *A. alata,* especially considering the observed positive correlation between its presence in raccoon dogs and wild boars.

Our data also indicate a clear upward trend in the threat posed by *A. alata* in wild boar towards the north of the country. This north-south gradient seems to be in line with the results of a previous study of the adult form of this parasite in foxes in Poland which indicated significant differences in prevalence between the northern regions (93.7% and 96.5%) and the southern regions (15.2% and 24.7%) (Karamon et al., 2018). The predicted prevalence in this study in the southern provinces did not exceed 10%, while all northern provinces showed a prevalence of over 20%, and even over 40% in north-eastern Poland. However, the model predicted a prevalence of over 100% for the Podlaskie province, suggesting the model did not have a good fit (Fig. 1.). Therefore, it should be stated that the large-scale analysis also has limitations resulting from the quality of the data used. The calculated prevalence was characterized in some provinces by a large range of confidence intervals resulting from the small sample size (e.g., for Zachodniopomorskie, the calculated prevalence was 42.9%, but CIs ranged from 6.2 to 79.5; for Podlaskie, the calculated prevalence was 41.7%, but CIs ranged from 13.8 to 69.6). Despite the uncertainty of estimation in our study, a similar north-south trend is also visible in the larger European context, with the percentage of positive results being generally higher in northern European countries than in southern ones. For example, the prevalence of *A. alaria* in wild boar samples, calculated based on the AMT method, was found to be 1.6%, 6%, 11.5%, 43.9% in Hungary, Austria, Germany and Latvia, respectively (Riehn et al., 2012; Paulsen et al., 2013; Berger and Paulsen, 2014; Ozoliņa et al., 2020). In Poland, the southern provinces presented a comparable calculated prevalence to Austria (6.8–7.7% for Małopolskie, Śląskie and Opolskie); the western provinces presented a similar prevalence to Germany (10.9% for Dolnośląskie and 14.1 for Opolskie); and the north-eastern provinces presented the highest prevalence in Poland, which is comparable to the prevalence in Latvia in some cases (for example, 43.3% in Warmińsko-Mazurskie province and 43.9% in Latvia). This trend is also visible among definitive hosts: the positive rates in red foxes were 78.7% in Poland and 94.8% in Lithuania (Bružinskaitė-Schmidhalter et al., 2012; Karamon et al., 2020), compared to 4.7% and 5.3% in Croatia and Italy, respectively (Rajković-Janje et al., 2002; Fiocchi et al., 2016). This trend is probably connected with the fact that northern countries offer generally better conditions for the complete cycle of *A. alata*, i.e., higher levels of wetland cover (Schleupner 2007).

It should be considered that areas with a particularly high percentage of infected wild boar may be subject to a local epizootic. Such areas should be prioritized for constant monitoring of *A. alata*. Particularly high infections of wild boar in a limited area have been described in Ireland (Murphy et al., 2012).

5. Conclusions

As our findings show, the occurrence of *A. alata* in wild boar requires multifactorial analysis. Environmental factors play a key role in risk assessment of *A. alata* in wild boar, therefore they should be taken in account when establishing meat inspection strategies and making possible recommendations to hunters in the face of a potential public threat. We recommend that selection of regions for meat inspection should include areas abundant with water and wetlands as well as those with higher local densities of foxes and raccoon dogs. In Poland, such meat inspections should first target northern provinces. A significant limitation occurs when predicting the risk of *A. alata* infection in small areas, which is probably the result of the large size of the home range of the studied animals.

Ethics approval and consent to participate

Not applicable.

Availability of data and material

The data supporting the conclusions of this article are included within the article. Raw data are available from the first author.

Funding

Not applicable.

Authors' contribution

DK: conceived, designed and coordinated the study; DK also carried out the study, the statistical analysis and drafted the manuscript. MN, JW: sample collection and laboratory work, manuscript review and editing. AD: drafted manuscript. ZB: sampling, manuscript review and editing. BP: data gathering and analysis. KA: coordinating the study, manuscript review and editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

Not applicable.

References

Berger, E.M., Paulsen, P., 2014. Findings of *Alaria alata* mesocercariae in wild boars (*Sus scrofa*, Linnaeus, 1758) in west Hungary (Transdanubia regions). Wien Tierarztl. Monatsschr 101, 120–123.

Bilska-Zając, E., Marucci, G., Piróg-Komorowska, A., Cichocka, M., Różycki, M., Karamon, J., Sroka, J., Bełcik, A., Mizak, I., Cencek, T., 2021. Occurrence of Alaria alata in wild boars (Sus scrofa) in Poland and detection of genetic variability between isolates. Parasitol. Res. Jan;120 (1), 83–91. https://doi.org/10.1007/s00436-020-06914-x. Epub 2020 Oct 26. PMID: 33103216; PMCID: PMC7846538.

Bružinskaitė-Schmidhalter, R., Šarkūnas, M., Malakauskas, A., Mathis, A., Torgerson, P. R., Deplazes, P., 2012. Helminths of red foxes (*Vulpes vulpes*) and raccoon dogs (*Nyctereutes procyonoides*) in Lithuania. Parasitology 139 (1), 120–127. https://doi.org/10.1017/S0031182011001715. Erratum in: Parasitol. 2012, 139(3), 418.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Inference: A Practical Information-Theoretic Approach, 2nd Edition. Springer-Verlag, New York. https://doi.org/10.1007/b97636.

Dollfus, R.P., Chabaud, A.G., 1953. *Distomum musculorum suis* H.C.J. Duncker 1896, mesocercaire d'*Alaria alata* (J.A.E. Goeze 1782), (Trematoda, Strigeata) chez un sanglier (*Sus scrofa* L. 1758, Fera) [*Distomum musculorum suis*, mesocercairia of *Alaria alata* in the wild boar Sus scrofa L]. Ann. Parasitol. Hum. Comp. 28 (5–6), 354–364 ([In French]).

Fattebert, J., Baubet, E., Slotow, R., Fischer, C., 2017. Landscape effects on wild boar home range size under contrasting harvest regimes in a human-dominated agro-ecosystem. Eur. J. Wildl. Res. 63 (2), 32.

Fiocchi, A., Gustinelli, A., Gelmini, L., Rugna, G., Renzi, M., Fontana, M.C., Poglayen, G., 2016. Helminth parasites of the red fox *Vulpes vulpes* (L., 1758) and the wolf Canis lupus Altobello, 1921 in Emilia-Romagna, Italy. Ital. J. Zool. 83, 503–513.

Gamble, H.R., Alban, L., Hill, D., Pyburn, D., Scandrett, B., 2019. International Commission on Trichinellosis: recommendations on pre-harvest control of *Trichinella* in food animals. Food Waterborne Parasitol 18 (15), e00039. https://doi.org/10.1016/j.fawpar.2019.e00039.

Górniak, A., Piekarski, K., 2002. Seasonal and multiannual changes of water levels in lakes of northeastern Poland. Pol. J. Environ. Stud. 11 (4), 349–354.

Jerina, K., Pokorny, B., Stergar, M., 2014. First evidence of long-distance dispersal of adult female wild boar (*Sus scrofa*) with piglets. Eur. J. Wildl. Res. 60 (2), 367–370.

Karamon, J., Dąbrowska, J., Kochanowski, M., Samorek-Pieróg, M., Sroka, J., Różycki, M., Bilska-Zając, E., Zdybel, J., Cencek, T., 2018. Prevalence of intestinal helminths of red foxes (*Vulpes vulpes*) in central Europe (Poland): a significant zoonotic threat. Parasites Vectors 11 (1), 436. https://doi.org/10.1186/s13071-018-3021-3.

Karamon, J., Sroka, J., Dąbrowska, J., Bilska-Zając, E., Skrzypek, K., Różycki, M., Zdybel, J., Cencek, T., 2020. Distribution of parasitic helminths in the small intestine of the red fox (*Vulpes vulpes*). Pathogens 9 (6), 477. https://doi.org/10.3390/pathogens9060477.

Keuling, O., Lauterbach, K., Stier, N., Roth, M., 2010. Hunter feedback of individually marked wild boar *Sus scrofa* L.: dispersal and efficiency of hunting in northeastern Germany. Eur. J. Wildl. Res. 56 (2), 159–167.

Keuling, O., Stier, N., Roth, M., 2008. Annual and seasonal space use of different age classes of female wild boar *Sus scrofa* L. Eur. J. Wildl. Res. 54 (3), 403–412, 1.

Klich, D., Sobczuk, M., Basak, S.M., Wierzbowska, I.A., Tallian, A., Hędrzak, M., Popczyk, B., Żoch, K., 2021. Predation on livestock as an indicator of drastic prey decline? The indirect effects of an African swine fever epidemic on predator–prey relations in Poland. Ecol. Indicat. 133, 108419.

Korpysa-Dzirba, W., Różycki, M., Bilska-Zając, E., Karamon, J., Sroka, J., Bełcik, A., Wasiak, M., Cencek, T., 2021. *Alaria alata* in terms of risks to consumers' health. Foods 10 (7), 1614. https://doi.org/10.3390/foods10071614.

Kramer, M.H., Eberhard, M.L., Blankenberg, T.A., 1996. Respiratory symptoms and subcutaneous granuloma caused by mesocercariae: a case report. Am. J. Trop. Med. Hyg. 55 (4), 447–448. https://doi.org/10.4269/ajtmh.1996.55.447.

Mauget, R., 1980. Home range concept and activity patterns of the European wild boar (*Sus scrofa* L.) as determined by radio tracking. In: A Handbook on Biotelemetry and Radio Tracking. Pergamon, Turkey, pp. 725–728.

McDonald, H.R., Kazacos, K.R., Schatz, H., Johnson, R.N., 1994. Two cases of intraocular infection with *Alaria* mesocercaria (Trematoda). Am. J. Ophthalmol. 117 (4), 447–455. https://doi.org/10.1016/s0002-9394(14)70003-0. Erratum in: Am J Ophthalmol 1994, 118(1), 129.

Möhl, K., Grosse, K., Hamedy, A., Wüste, T., Kabelitz, P., Lücker, E., 2009. Biology of *Alaria* spp. and human exposition risk to *Alaria* mesocercariae-a review. Parasitol. Res. 105 (1), 1–15. https://doi.org/10.1007/s00436-009-1444-7.

Murphy, T.M., O'Connell, J., Berzano, M., Dold, C., Keegan, J.D., McCann, A., Murphy, D., Holden, N.M., 2012. The prevalence and distribution of *Alaria alata,* a potential zoonotic parasite, in foxes in Ireland. Parasitol. Res. 111 (1), 283–290. https://doi.org/10.1007/s00436-012-2835-8.

Ozoliņa, Z., Bagrade, G., Deksne, G., 2018. The host age related occurrence of *Alaria alata* in wild canids in Latvia. Parasitol. Res. 117 (12), 3743–3751. https://doi.org/10.1007/s00436-018-6074-5.

Ozoliņa, Z., Deksne, G., Pupins, M., Gravele, E., Gavarane, I., Kirjušina, M., 2021. *Alaria alata* mesocercariae prevalence and predilection sites in amphibians in Latvia. Parasitol. Res. 120 (1), 145–152.

Ozoliņa, Z., Mateusa, M., Šuksta, L., Liepiņa, L., Deksne, G., 2020. The wild boar (*Sus scrofa*, Linnaeus, 1758) as an important reservoir host for *Alaria alata* in the Baltic region and potential risk of infection in humans. zVet. Parasitol. Reg. Stud. Rep. 22, 100485. https://doi.org/10.1016/j.vprsr.2020.100485.

Patrelle, C., Portier, J., Jouet, D., Delorme, D., Ferté, H., 2015. Prevalence and intensity of *Alaria alata* (Goeze, 1792) in water frogs and brown frogs in natural conditions. Parasitol. Res. 114 (12), 4405–4412. https://doi.org/10.1007/s00436-015-4680-z.

Paulsen, P., Forejtek, P., Hutarova, Z., Vodnansky, M., 2013. *Alaria alata* mesocercariae in wild boar (Sus scrofa, Linnaeus, 1758) in south regions of the Czech Republic. Vet. Parasitol. 197 (1–2), 384–387. https://doi.org/10.1016/j.vetpar.2013.05.024.

Pestál, K., 1989. První nález *Agamodistomum suis* (STILES, 1908) u cernězvěrě v CSSR. [The first finding of *Agamodistomum suis* (STILES, 1908) in black clover in the CSSR]. Veterinarstvi 39, 437–439 (in Czech).

Portier, J., Jouet, D., Ferté, H., Gibout, O., Heckmann, A., Boireau, P., Vallée, I., 2011. New data in France on the trematode *Alaria alata* (Goeze, 1792) obtained during *Trichinella* inspections. Parasite 18 (3), 271–275. https://doi.org/10.1051/parasite/2011183271.

Portier, J., Jouet, D., Vallée, I., Ferté, H., 2012. Detection of *Planorbis planorbis* and *Anisus vortex* as first intermediate hosts of *Alaria alata* (Goeze, 1792) in natural conditions in France: molecular evidence. Vet. Parasitol. 190 (1–2), 151–158. https://doi.org/10.1016/j.vetpar.2012.06.020.

Rajković-Janje, R., Marinculić, A., Bosnić, S., Benić, M., Vinković, B., Mihaljević, Ž., 2002. Prevalence and seasonal distribution of helminth parasites in red foxes (*Vulpes vulpes*) from the Zagreb County (Croatia). Z. Jagdwiss. 48, 151–160.

Ramisz, A., Balicka-Ramisz, A., 2001. The prevalence of *Alaria alata* in red foxes (*Vulpes vulpes* L.) in the western part of Poland. Tierärztliche Umsch. 56, 423–425.

Rentería-Solís, Z.M., Hamedy, A., Michler, F.U., Michler, B.A., Lücker, E., Stier, N., Wibbelt, G., Riehn, K., 2013. *Alaria alata* mesocercariae in raccoons (*Procyon lotor*) in Germany. Parasitol. Res. 112 (10), 3595–3600. https://doi.org/10.1007/s00436-013-3547-4.

Rentería-Solís, Z., Kołodziej-Sobocińska, M., Riehn, K., 2018. *Alaria* spp. mesocercariae in Eurasian badger (*Meles meles*) and wild boar (*Sus scrofa*) from the Białowieża Forest, north-eastern Poland. Parasitol. Res. 117 (4), 1297–1299. https://doi.org/10.1007/s00436-018-5819-5.

Riehn, K., Hamedy, A., Grosse, K., Zeitler, L., Lücker, E., 2010. A novel detection method for Alaria alata mesocercariae in meat. Parasitol. Res. 107 (1), 213–220. https://doi.org/10.1007/s00436-010-1853-7. Epub 2010 Apr 20. PMID: 20405145.

Riehn, K., Hamedy, A., Grosse, K., Wüste, T., Lücker, E., 2012. *Alaria alata* in wild boars (*Sus scrofa*, Linnaeus, 1758) in the eastern parts of Germany. Parasitol. Res. 111 (4), 1857–1861. https://doi.org/10.1007/s00436-012-2936-4.

Riehn, K., Hamedy, A., Saffaf, J., Lücker, E., 2013. First interlaboratory test for the detection of *Alaria* spp. mesocercariae in meat samples using the *Alaria* spp. mesocercariae migration technique (AMT). Parasitol. Res. 112 (7), 2653–2660. https://doi.org/10.1007/s00436-013-3432-1.

Sailer, A., Glawisching, W., Irschik, I., Lücker, E., Riehn, K., Paulsen, P., 2012. Findings of *Alaria alata* mesocercariae in wild boar in Austria: current knowledge, identification of risk factors and discussion of risk management options. Wien. Tierärztliche Mon. 99, 346–352.

Schleupner, C., 2007. Estimation of Spatial Wetland Distribution Potentials in Europe. FNU-135. Centre for Marine and Atmospheric Science. Hamburg University.

Shimalov, V.V., Shimalov, V.T., 2001. Helminth fauna of the American mink (*Mustela vison* Schreber, 1777) in Belorussian Polesie. Parasitol. Res. 87 (10), 886–887.

Sodeikat, G., Pohlmeyer, K., 2002. Temporary home range modifications of wild boar family groups (*Sus scrofa* L.) caused by drive hunts in Lower Saxony (Germany). Z. Jagdwiss. 48 (1), 161–166.

Strokowska, N., Bełkot, Z., Wiśniewski, J., Nowicki, M., Didkowska, A., Anusz, K., Szkucik, K., 2021a. Infestation of wild boar meat from the Eastern Lublin province with *Alaria* mesocercariae. Med. Weter. 77 (12), 588–593.

Strokowska, N., Nowicki, M., Klich, D., Bełkot, Z., Wiśniewski, J., Didkowska, A., Chyla, P., Anusz, K., 2020. The occurrence of *Alaria alata* mesocercariae in wild boars (*Sus scrofa*) in north-eastern Poland. Int. J. Parasitol. Parasites Wildl. 12, 25–28. https://doi.org/10.1016/j.ijppaw.2020.04.006.

Strokowska, N., Nowicki, M., Klich, D., Didkowska, A., Filip-Hutsch, K., Wiśniewski, J., Bełkot, Z., Anusz, K., 2021b. A comparison of detection methods of *Alaria alata* mesocercariae in wild boar (*Sus scrofa*) meat. Int. J. Parasitol. Parasites Wildl. 16, 1–4.

Takeuchi-Storm, N., Al-Sabi, M.N., Thamsborg, S.M., Enemark, H.L., 2015. *Alaria alata* mesocercariae among feral cats and badgers, Denmark. Emerg. Infect. Dis. 21 (10), 1872–1874. https://doi.org/10.3201/eid2010.141817.

Tylkowska, A., Pilarczyk, B., Pilarczyk, R., Zyśko, M., Tomza-Marciniak, A., 2018. The presence of *Alaria alata* fluke in the red fox (*Vulpes vulpes*) in the north-western Poland. Jpn. J. Vet. Res. 66, 203–208.

Voelkel, A.C., Dolle, S., Koethe, M., Haas, J., Makrutzki, G., Birka, S., Lücker, E., Hamedy, A., 2019. Distribution of Alaria spp. mesocercariae in waterfrogs. Parasitol. Res. 118 (2), 673–676. https://doi.org/10.1007/s00436-018-6133-y.

Wójcik, A.R., Franckiewicz-Grygon, B., Zbikowska, E., 2001. Badania nad inwazja *Alaria alata* (Goeze, 1782) w województwie kujawsko-pomorskim [The studies of the invasion of *Alaria alata* (Goeze,1782) in the Province of Kuyavia and Pomerania]. Wiad. Parazytol. 47 (3), 423–426 (In Polish).