Research article

Resource-driven changes in wild boar movement and their consequences for the spread of African Swine Fever in the Russian Far East

Scott J. Waller[1], **Kevin Morelle**[2], **Ivan V. Seryodkin**[3], **Alexander N. Rybin**[4], **Svetlana V. Soutyrina**[5], **Alain Licoppe**[6], **Mark Hebblewhite**[7] and **Dale G. Miquelle**[1]

[1]Wildlife Conservation Society, New York, NY, USA
[2]Max Planck Institute of Animal Behavior, Radolfzell, Germany
[3]Pacific Institute of Geography, Far Eastern Branch of the Russian Academy of Sciences, Vladivostok, Russia
[4]ANO WCS, Vladivostok, Russia
[5]Sikhote-Alin Biosphere Zapovednik, Terney, Russia
[6]Department of Natural and Agricultural Environment Studies, Public Service of Wallonia, Gembloux, Belgium
[7]Wildlife Biology Program, University of Montana, Missoula, MT, USA

Correspondence: Scott J. Waller (swaller@wcs.org)

Knowledge of animal movement patterns is invaluable to understanding the spread of diseases among wildlife populations. One example is the recent African swine fever (ASF) outbreak among wild boar *Sus scrofa* populations across East Asia, where there is a lack of information on movements of this species. During a wild boar tracking project to inform abundance estimation methods in the Russian Far East's Sikhote-Alin Biosphere Zapovednik, the combination of high variability in pulsed resources of acorns and pine nuts between fall 2019 and fall 2020, and the outbreak of ASF during the latter year, offered the unique opportunity to investigate the relationship between wild boar movements to exploit pulsed resources and the potential for disease spread. We analyzed relocation data from GPS-collared wild boar in fall 2019 and 2020 and compared them to reference data in Belgium, representative of western Europe. We found remarkable differences in movement patterns, with Far East wild boar travelling large distances in fall 2020 (maximum observed of 77 km in four days) when the availability of acorns was low. In our resource selection analysis, we found clear selection for mast-producing forest types that corresponded with the species of greater mast production (oak or pine) for that year. Comparing the displacement of individual wild boar along a moving window of 1–7 days (time between infection and the onset ASF symptoms) highlighted the potential of rapid ASF spread over long distances when wild boar are in search of pulsed resources. This work demonstrates the capacity of wild boar to move long distances to exploit resources and emphasizes the need to consider resource availability when predicting the speed and extent to which diseases such as ASF can spread.

www.wildlifebiology.org

Introduction

Knowledge of animal movement patterns can provide an understanding of the potential for a disease to spread when infection occurs by contact between individuals or between individuals and the contaminated environment (Dougherty et al. 2018, Pepin et al. 2022, Wilber et al. 2022). Patterns of animal movement are largely determined by the search for resources (Altizer et al. 2011, Hooten et al. 2017), so understanding the distribution of resources through time and space is key for predicting movement behavior. Information provided by resource selection analyses is therefore of great value to disease managers as a tool to both plan for and prevent disease spread.

One such example, illustrating the intricacies between resources distribution, disease, and animal movement, can be found in the wild boar *Sus scrofa*–African Swine Fever (ASF) host–disease system. ASF is an ecologically and economically dramatic disease affecting domestic pig and wild boar populations worldwide (Guberti et al. 2022). This deadly hemorrhagic disease can result in 95% mortality of infected wild boar populations (Morelle et al. 2020, O'Neill et al. 2020, Waller et al. 2022). In Europe, ASF spreads at a relatively slow pace and is driven by seasonality, landscape structure, and population density (EFSA et al. 2018, Podgórski and Śmietanka 2018, Taylor et al. 2020). Movements of wild boar are unlikely to explain the spread of ASF in Europe into uninfected regions due to: 1) the relative sedentary nature of wild boar, which rarely travel further than 10 km (Prévot and Licoppe 2013, Taylor et al. 2020); and 2) the disease severity – infected animals usually die within 1–2 weeks of exposure, even further reducing the likelihood of highly sedentary animals dispersing a disease over any significant distances (Podórski and Śmietanka 2018, Morelle et al. 2023). Instead, the long-distance spread of ASF in Europe has been human-mediated, as exemplified by cases of ASF in Belgium and the Czech Republic (Sauter-Louis et al. 2022).

In east Asia, the arrival of ASF puts the livelihoods of local human communities at risk (Denstedt et al. 2021), threatens endangered species of the Suidae family (Luskin et al. 2020), and reduces the availability of wild boar as a critical prey resource for carnivores such as the tiger *Panthera tigris* (Hayward et al. 2012). Because there is little to no information on movements of wild boar in Asia, movement rates estimated in Europe are often used as reference by managers in Asia during their assessments of rates of spread of ASF virus (Guberti et al. 2022). But recent evidence from the Russian Far East (Zakharova et al. 2021, Shotin et al. 2022) has shown a much quicker spread of ASF in the region. The authors cite low biosecurity of the majority of small-holder pig farms as a key reason, which enables more frequent domestic pig–wild boar contact. Another potential reason is the vast extent of relatively intact forests in temperate Asia where human

population density and anthropogenic disturbances are low and wild boar can therefore move largely unimpeded. For example, in the Sikhote-Alin Mountains, decades of anecdotal evidence by hunters and scientists describe wild boar traveling great distances in short periods of time to exploit the production of pulsed resources of Mongolian oak *Quercus mongolica* acorns along the coast and Korean pine *Pinus koraeinsis* nuts further inland (Bromley and Kucherenko 1983, Heptner et al. 1988); however, no empirical evidence that we are aware of exists to confirm or dispute these claims. Such movements would call into question the applicability of movement rates estimated in Europe to understand the spread of ASF in entirely different ecological contexts such as the Russian Far East.

During a wild boar GPS tracking project to inform abundance estimation methods in the Sikhote-Alin Biosphere Zapovednik (2018–2021), two important events occurred that added unanticipated value to this dataset. First, we observed a reduction in acorn production in fall 2020 compared to fall 2019. In other study systems, decreased availability of pulsed resources like acorns has been shown to increase both wild boar home range size and finer-scale movement rates (Singer et al. 1981, Morelle et al. 2015, Bisi et al. 2018). Secondly, ASF was also detected in wild boar near our study area in September 2020 (OIE 2020), and many of our GPS-collared wild boar died after the arrival of the disease. These events provided the opportunity to understand how wild boar movement in the Far East responds to varying mast availability, and how these responses may influence the spread of ASF.

In this study, we aimed to better understand the relationship between wild boar movements to exploit pulsed resources and the potential for disease spread – what we call the 'resource–movement–disease cascade' – by answering two questions: 1) how did variability in pulsed resources during fall 2019 and fall 2020 influence the movement behavior of wild boar in the Russian Far East? And 2) what are the implications of this influence for the spread of ASF by wild boar to previously uninfected areas? To answer these questions, we conducted a largely descriptive analysis of wild boar movement in the Sikhote-Alin Biosphere Zapovednik during these two years of respectively high and low availability in the pulsed resources of acorns and pine nuts, and compared these with movements of a wild boar population living in another continent and in a different environmental context in Belgium, representative of western Europe. We analyzed the resource selection process to better understand what resources were driving movements during each year. We then considered the implications of the observed movement behavior for the spread rate of ASF virus. Though we were limited by small sample size, we used our results to help evaluate whether the current understanding of the relationship between wild boar movement and the spread of ASF into

uninfected areas – especially in places like the Russian Far East with large tracts of undeveloped, mast-producing forests – should be reconsidered.

Material and methods

Study area

Sikhote-Alin Biosphere Zapovednik (45.0490°N, 136.6203°E), an IUCN Category Ia nature reserve, lies in the central Sikhote-Alin Mountains of the Russian Far East (Fig. 1). Summers in the low-elevation Sikhote-Alin Mountains (most peaks are < 800 m a.s.l.) are hot and wet while winters are cold and dry. The landscape of the Zapovednik is heavily forested, predominately with Mongolian oak along the coast of the Sea of Japan and with mixed forests of broadleaf species such as Costata birch *Betula costata*, Amur linden *Tilia amurensis*, and Manchurian ash *Fraxinus mandschurica*, growing together with Korean pine further inland (Krestov 2003). At higher elevations, forests consist of predominantly conifer species such as spruce *Picea* spp. and fir *Abies* spp. The heterogeneous distribution of both coastal Mongolian oak and inland Korean pine forests results

in important spatial and temporal variation in the availability of acorns and pine nuts. The quality and quantity of these mast crops is somewhat cyclical (both nuts ripen in the fall, but years of abundant production are usually followed by one or more years of low productivity), but productivity in any given year is highly unpredictable.

Wild boar captures

From spring 2019 to winter 2020–2021, we captured and collared 13 adult female wild boars in the southern and central parts of Sikhote-Alin Zapovednik using wooden corral traps baited with dried, shelled corn. We used a combination of tiletamine-zolazepam (Telazol brand, 6.0–9.2 mg kg^{-1}) and medetomidine (0.07 mg kg^{-1}) to anesthetize female wild boar before fitting them with Lotek GPS Litetrack 420 Iridium collars. These were set to a 1 h fix interval schedule between 1 April and 1 November, then a 15 min fix interval schedule between 1 November and 1 April. We only collared adult females because the necks of males are often thicker than their heads, and young/subadults grow quickly. All captures and handling were conducted by WCS and Zapovednik staff, including oversight of a veterinarian at every capture, and
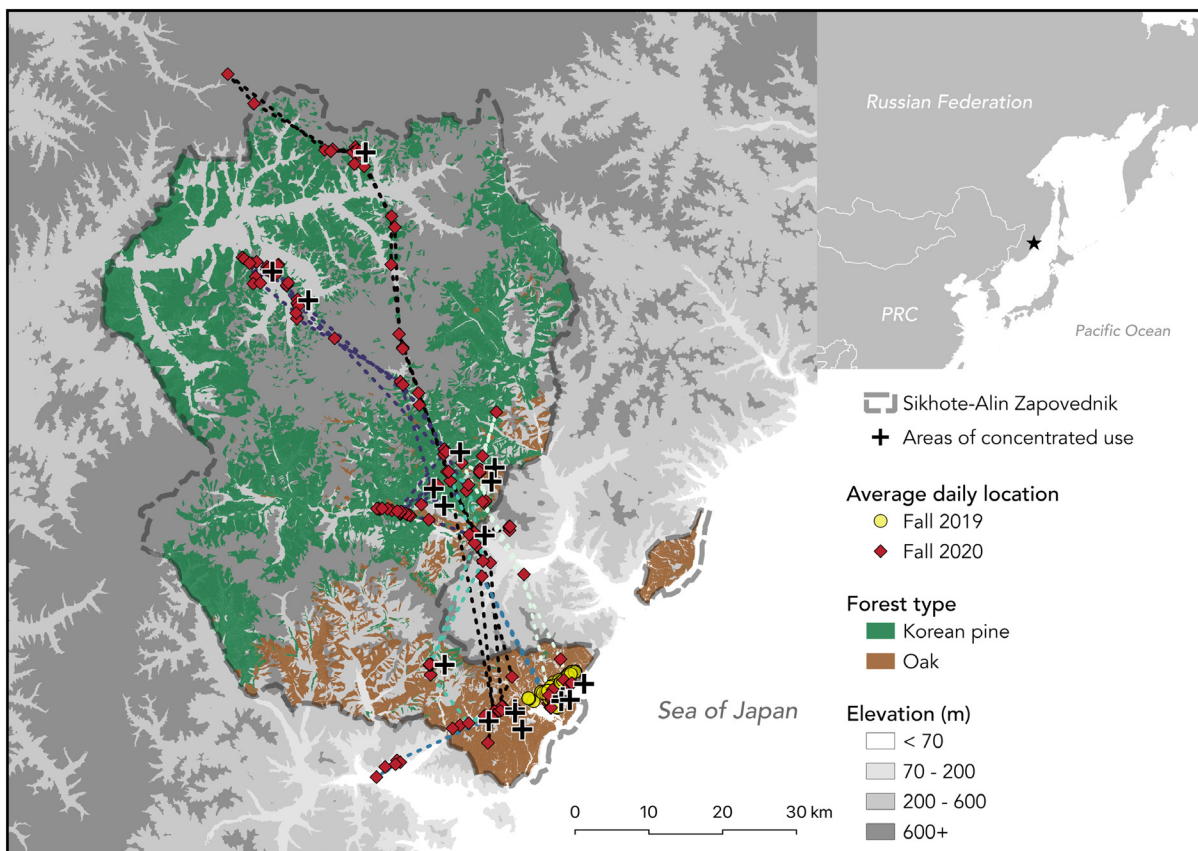

Figure 1. Map of our study area in the Sikhote-Alin Biosphere Zapovednik, Russian Far East. The distribution of oak and pine forests is shown in brown and green. Average daily locations of wild boar in fall 2019 (n = 2) and fall 2020 (n = 5) are shown by yellow circles and red diamonds. The straight-line paths between daily locations (averaged x–y coordinates) of each individual are shown with colored, dashed lines. Areas of concentrated use, where we analyzed resource selection, are shown as black crosses.

met IACUC animal care standards as approved by the Univ. of Montana (AUP 061-19).

Movement data processing

We were most interested in wild boar movement behavior and resource selection at the beginning of the masting period (early-mid fall), when acorns and/or pine nuts may have driven long-distance movements (defined in 'Characterizing movement patterns' sub-section, below) that have the greatest potential to spread ASF. We therefore calculated a separate period of analysis for each individual based on the average number of days they spent at concentrated use areas, adjusted to the beginning and end of their long-distance movement behavior. If an individual did not make any long-distance movements, we calculated a time window starting from the average commencement date of the long-distance movements of other wild boar, and extending for an average duration of such observed behavior in other individuals. Such an approach aimed to prevent the over-representation of data from periods outside of potential significant movement (which could weaken the selection strength for forest types that might be driving long-distance movements).

To be consistent, we resampled the locations collected every 15 min (i.e. any locations from November through March) on an hourly basis. Fix rates were generally poor, averaging 48% missing locations across individuals during the period of analysis. We removed locations in which the dilution of precision (DOP) was greater than 15, which represented an error radius of roughly > 50 m based on calibration data from one of the collars.

Because guiding documents for ASF management (Guberti et al. 2022) are based on wild boar movement observations in Europe, we compared movement patterns of wild boar tracked in the Russian Far East with those from a large dataset of GPS-collared wild boar representative of the western European context. We used movement data from southern Belgium, with 33 individuals tracked between 2006 and 2017 in different study sites which varied in plant composition and structure, from highly forested to more open agricultural landscapes (Prévot and Licoppe 2013, Morelle 2015). According to the study sites, animals were caught using 2 × 1 m transportable cages, corrals traps, and vertical nets. Animals were anesthetized and fitted with GPS/GSM Plus 3D collar Vectronic collars (Vectronics Aerospace GmbH, Berlin, Germany). Please refer to Prévot and Licoppe (2013) and Morelle (2015) for more details on captures in Belgium, and to the Supporting information for a summary of the data used in this analysis. To make our comparison of movement metrics sound, we analyzed data from Belgium over the same monitoring period as our data (i.e. from early September to mid-October).

GPS-based movement metrics

To characterize the movement behavior of GPS-collared wild boar, we calculated three movement metrics for individuals based on the average x–y coordinate for each day: 1) daily displacement, 2) maximum displacement, and 3) intensity of use. We conducted these analyses using R statistical software (ver. 4.2.2; www.r-project.org) in R Studio (Posit team 2023), and all of the metrics we used relied on functions provided by the 'amt' package (Signer et al. 2019). Daily displacement simply measured the distance between the average x–y locations of individual boar between two consecutive days. This averaged daily straight-line distance describes how far wild boar generally moved each day while allowing for the comparison with data from Belgium where collars had different fix schedules (median = 1 h; max = 12 h) and success rates. Daily travel distance might have been a more illustrative measurement of movement behavior; but due to our low fix rates compared to the temporal autocorrelation scale of the relocation data, which biases estimates (Noonan et al. 2019), we ultimately chose to use daily displacement instead. We tested for significant differences in daily displacement distributions between fall 2019, fall 2020, and Belgium using non-parametric Wilcoxon rank-sum tests. Maximum displacement measured the straight-line distance between a wild boar's first location and its furthest location from that point during the mast production period (i.e. its furthest displacement during all days of the analysis). Intensity of use was calculated by the ratio of the sum of daily displacements (i.e. estimated by summing all straight-line distances between average daily locations) and the square root of the minimum convex polygon drawn around all locations (Loretto and Vieira 2005, Almeida et al. 2010). The more intensely an animal used an area (i.e. the more tortuous its movements path), the higher the intensity of use.

Characterizing movement patterns of wild boar during the mast production period

In observing movements of collared wild boar during the fall mast production period, there appeared to be two primary types of movement. Wild boar would often concentrate within a relatively small area for multiple days, but in some instances would make extensive, long-distance movements to new 'concentrated use areas.' To test and categorize these movement types, we defined concentrated use areas as locations where the displacement between a wild boar's daily averaged locations was less than 7 km for at least a two-day period. An individual was therefore considered to have left this concentrated use area and entered a period of long-distance movement if it traveled at least 7 km in 24 h from the last location at that area. We chose 7 km as a threshold because this is outside the interquartile range and towards the tail of the daily displacement distribution of both years. Utilizing the 'moveVis' package (Schwalb-Willmann et al. 2020), we further visually verified GPS-collared wild boar movement behaviors to distinguish between concentrated use areas and extensive movements between these sites.

Drivers of movement

We wanted to understand the influence of forest type composition on wild boar movement patterns. More specifically, we aimed to answer two questions: 1) if wild boar made

long-distance movements, what made them change this behavior and stop at a particular concentrated use area? 2) at those concentrated use areas, what resources did they select? To answer the first question, we evaluated changes in forest types along wild boar movement paths that may have been associated with transitions from long-distance movements to localized foraging. First, we visually inspected the forest types through which wild boar travelled during their long-distance movements. For each day since 'departure' (i.e. when wild boar left their concentrated use area and started their long-distance movements), we calculated the daily centroid of relocations, then drew a circle with a radius delineated by the standard deviation of distances of each location from that day's centroid. Within this circle, we assess the proportion of each forest type by annotating locations with a spatial dataset that identified 15 forest types provided by the Zapovednik. We collapsed the original 15 categories of forest type into four main categories to better represent mast-producing forests: 1) forests of predominately Mongolian oak; 2) forests of predominately Korean pine; 3) other forest types (such as spruce–fir); and 4) other landcover types (such as seashore and talus). We then plotted the relative proportion of forest types for each day together with the duration at each concentrated use area to evaluate what changes in forest type may have initiated a period of concentrated use.

To answer the second question, we used resource selection functions (RSF) and a used-available framework (Manly et al. 2002) to assess the relative selection strength for different forest types at concentrated use areas during fall 2019 and fall 2020. Available locations were randomly generated within the minimum convex polygons drawn around used locations at a concentrated use area, with 10 available locations sampled for every used location to adequately represent the available forest types. We used logistic regression (Hosmer and Lemeshow 2000) to model the relative selection strength of forest types for each year. We treated 'other' forest types as our reference category so that selection coefficients represented the selection strength of oak forests, pine forests, and non-forest landcover types relative to other forest types. Available locations were weighted to ensure unbiased and stable estimates of selection coefficients (Fithian and Hastie 2013, Muff et al. 2020, Fieberg et al. 2021). We included mixed effects (both random intercepts and slopes) to account for serial and spatial correlation in locations at each concentrated use area (Gillies et al. 2006, Muff et al. 2020). This also ensured that the standard errors of estimated coefficients were not overly precise and better represented variation in selection across concentrated use areas (Schielzeth and Forstmeier 2009, Muff et al. 2020). Initial attempts to estimate parameters by maximizing the likelihood failed to converge, likely due to small sample size. We therefore used a Bayesian approach to develop posterior distributions of the parameters using a Hamiltonian Monte Carlo sampler as provided by the 'brms' package in R (www.r-project.org, Bürkner 2017). We used uninformed priors since no similar analysis of wild boar resource selection at this scale of selection had been conducted in our study region, and we wished for parameter estimates to be driven solely by

our data. After running 4 chains of the sampler, we assessed agreement of parameter estimates across chains using the metric $\hat{R}$, with recommended values of $\hat{R} < 1.01$ indicating convergence both between and within chains (Vehtarh et al. 2021). Finally, we used k-folds cross validation to determine the predictive strength of our RSFs (Boyce et al. 2002). In fall 2020 (n = 5), we left one individual out for each iteration, then fit an RSF to data from the remaining individuals. We used the estimated coefficients from that model to predict the relative probability of use for each used location of the individual left out. After creating bins based on quantiles of predicted relative probabilities of use, we tallied the number of used locations that fell within each bin. Because we only had data from 2 individuals in fall 2019, we combined their data, then used a training-testing ratio of 20% for cross validation (Boyce et al. 2002). If our RSF had high predictive strength, then the Spearman rank-correlation between the bin rank and the number of used locations would be strongly positively correlated. After estimating correlation coefficients for each iteration, we produced a final correlation coefficient, r_s, that was the average of all correlation coefficients. For the fall 2020 RSF, this was also weighted by the proportion that each individual boar for which we generated predictions contributed to the total amount of relocation data.

Estimates of displacement potential while infectious

To investigate how far individual wild boar could potentially travel while infected with the ASF virus, we measured the maximum displacement of individual wild boar over increasing periods of time corresponding with the incubation time (3–7 days) for the relevant isolate of ASF virus (ASFV/Primorsky 19/WB6723; Shotin et al. 2022). Note that this analysis included all location data during the period of analysis for each individual (Table 1), not just locations during long-distance movements. While the sample size in Shotin et al. (2022) was small, the authors nevertheless provided the best evidence for the range of time pigs may be infected with ASF virus, but not yet be symptomatic. Accordingly, we estimated the maximum displacement distance of individual wild boar during the fall 2019 and fall

Table 1. Description of the data and period of analysis for each collared wild boar in the Russian Far East. 'ID' represents the unique collar ID assigned to each wild boar. See Methods subsection 'Period of analysis'. 'n fixed locations' describes the number of locations with x–y coordinates at a sufficient precision (DOP < 15). 'n CUAs' counts how many concentrated use areas (CUAs) were identified for each individual wild boar.

Year	ID	Period of analysis	n fixed locations	n CUAs
Fall 2019	83534a	1 Oct–1 Nov	384	1
	83535a	1 Oct–1 Nov	115	1
Fall 2020	83531a	11 Sep–26 Oct	400	5
	83532a	18 Sep–15 Nov	1224	6
	83534b	27 Sep–10 Oct	140	2
	83535b	29 Sep–15 Oct	192	3
	83537c	29 Sep–21 Oct	328	4

2020 over periods of 1–7 days. Estimates of maximum displacement were made starting on consecutive days for each individual, as each day represented a potential new date of infection during this exercise. We calculated the maximum displacement from consecutive days for each individual and year, then estimated the collective median, 75th, 90th and 100th percentiles of each year. We compared these summary statistics between years and assessed how these different summaries of wild boar movement (e.g. looking at median displacement versus 90th percentile displacement) imply different risks of the spread of ASF.

Results

GPS-based movement metrics

The number of days analyzed for each wild boar ranged from 14–59 (Table 1). Wild boar tracked in fall 2020 traveled much greater distances than wild boar in fall 2019 or from Belgium (Table 2). Median displacement was significantly different between fall 2019 and fall 2020 ($W = 2065$, $p < 0.001$), fall 2019 and Belgium ($W = 53540$, $p < 0.001$), and fall 2020 and Belgium ($W = 184\ 159$, $p < 0.001$). Median daily displacement in fall 2020 was roughly three-times greater than in 2019 and ten-times greater than in Belgium. The difference in the maximum displacement was even greater, with one individual in fall 2020 reaching a displacement of 93.4 km from her location at the start of this analysis. This is over 14 times greater than the maximum displacement of individuals from the year before, while some 16 times greater than the maximum displacement observed in Belgium (Table 2). Wild boar tracked in fall 2020 generally used the area of their range less intensely than those from the year before, though this metric varied substantially. In Belgium, the intensity of use varied widely, from 5 to 40. The highest level of intensity of use in this study population was over 4 times greater than any level recorded in the Russian Far East.

Patterns and drivers of movement during the mast production period

In fall 2019, each wild boar only used one area of concentrated use; they did not make any movements leading to a displacement of more than 7 km in 24 h. In fall 2020, we identified 22 concentrated use areas, ranging in length from 2 to 18 days. Two of these were excluded from further analysis

because most locations were outside the Zapovednik and therefore lacked spatial information on forest type. Looking at changes in forest type between concentrated use areas in fall 2020, wild boar moved between oak and pine forests during their long-distance travels (Fig. 2). For three individuals, the second concentrated use area (after their first long-distance movement) followed shortly after a sharp transition from predominantly oak forests to those with at least ~ 50% Korean pine. We note that the second concentrated use areas of the other two individuals (83531a and 83534b, Fig. 2) that fell outside the Zapovednik – the two concentrated use areas we excluded as mentioned above – were predominantly forests of Korean pine as well, based on our own knowledge of those areas.

When estimating the coefficients of our RSFs, all chains resulted in an R̂ of 1.01 or 1.00, indicating sufficient convergence across chains. In fall 2019, wild boar were 1.4 times more likely to select oak forests over non-masting forests (($\beta_{oak} = 0.36$, 95% CI [0.17–0.54]) and strongly avoided non-forest cover types ($\beta_{nonforest} = -2.49$, 95% CI [−2.92 to −2.09]). No used or available locations fell within forests of predominantly Korean pine. Because there was only 1 area of concentrated, continual use for each individual, we did not include a random effect. K-folds cross validation indicated this generally strong prediction strength of this model (average $r_s = 0.85$, range: 0.66–0.96). The next year, wild boar strongly selected Korean pine forests at concentrated use areas ($\beta_{pine} = 0.57$, 95% CI [0.10–1.08]), and weakly avoided oak forests ($\beta_{oak} = -0.18$, 95% CI [−0.86–0.50]) and non-forest cover types ($\beta_{nonforest} = -0.26$, 95% CI [−1.46–0.60]) relative to non-masting forests ($\beta_0 = -7.15$, 95% CI [−7.61 to −6.74]). There was some variation in selection strength for different forest and non-forest types between areas of concentrated use, as demonstrated by the wide confidence intervals reported above (see also the forest plots in the Supporting information). The only forest type with consistent positive selection by wild boar was Korean pine. Our k-folds cross validation found that this model generally did well at predicting out-of-sample wild boar used locations (average $r_s = 0.71$), though predictive success varied considerably depending on the individual left out (r_s range: 0.41–0.89).

Estimates of displacement potential while infectious

We found considerable differences in the distance traveled by wild boar during fall 2019 and fall 2020 over periods of 1 to 7 days (Fig. 3). In fall 2019, wild boar did not travel

Table 2. Summary of movement metrics by wild boar captured during the fall 2019 and fall 2020 within Sikhote-Alin Zapovednik, and from example European study populations in Belgium. 'Daily displacement' measures the straight-line distance between the average x–y coordinates of individuals each day. 'Max displacement' measures the maximum straight-line distance between the starting location for an individual and its furthest location from that point during the period of analysis. 'Intensity of use' is the ratio of the total distance traveled over the square root of the minimum convex polygon drawn around all locations. See 'GPS-based movement metrics' in Methods for further details.

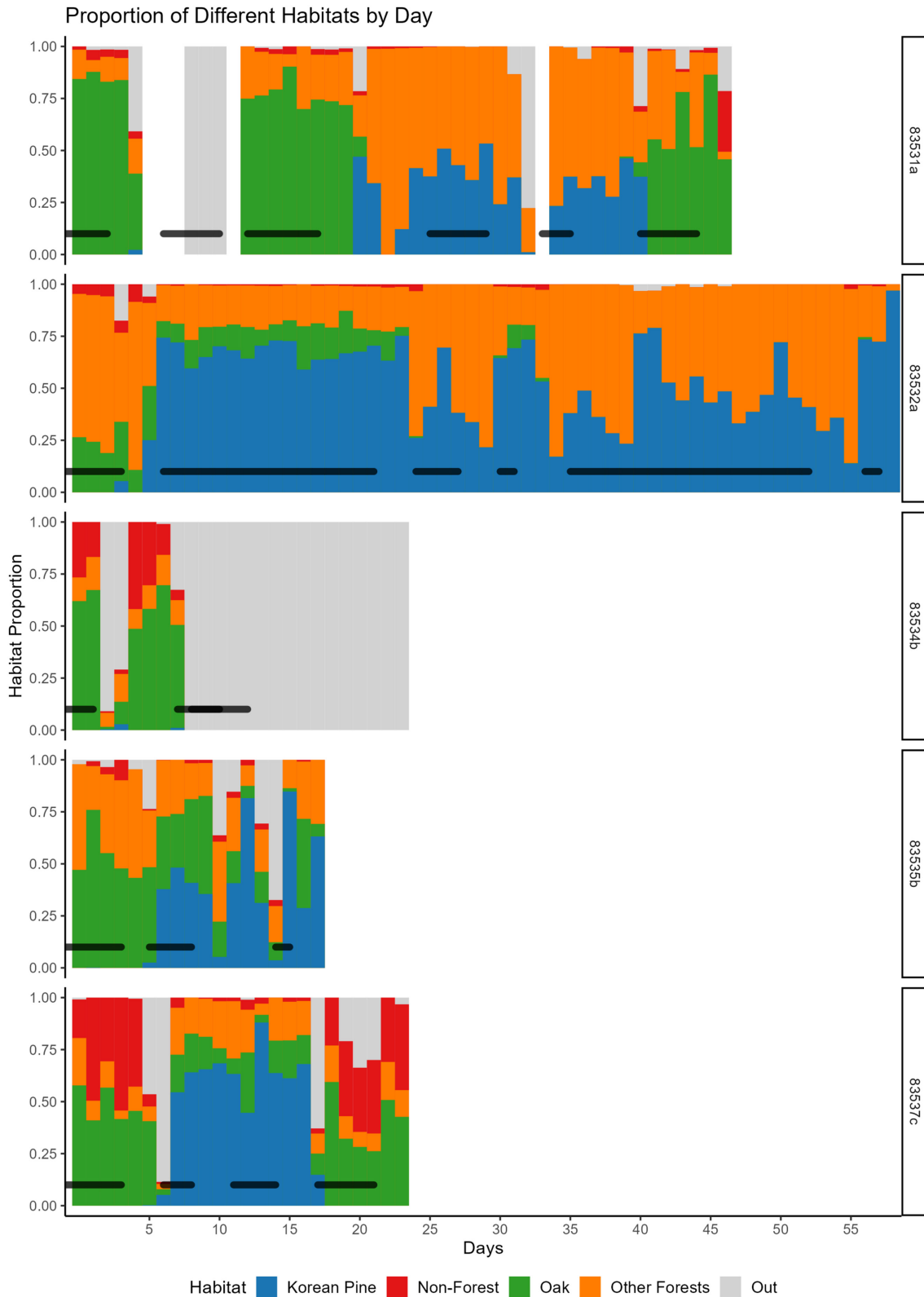| Study group	Daily displacement (median, km)	Max displacement (km)	Intensity of use (min–max)
Fall 2019 (n = 2)	0.92 [95% CI: 0.03–3.03]	6.9	10.26–10.69
Fall 2020 (n = 5)	2.86 [95% CI: 0.07–21.98]	93.4	4.47–12.35
Belgium (n = 33)	0.28 [95% CI: 0.44–0.50]	5.8	5.71–39.7

Figure 2. Changes in the proportion of cover type as wild boar traveled during fall 2020 and their relation to areas of concentrated use. The colors in the legend represent the different cover types. The grey sections ('out') indicate when locations fell outside of the Zapovednik and thus lacked information on cover type. Black lines indicate the duration of successive stopover sites for each individual. The x-axis represents the number of days since the start of each wild boar's concentrated use behavior. See the Methods section for more details on how we defined and identified these areas.
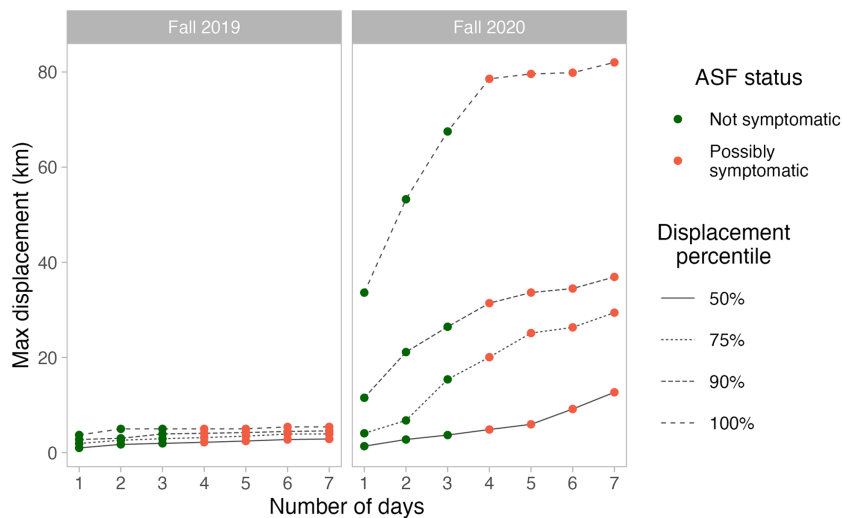
Figure 3. Maximum displacement of wild boar in the Sikhote-Alin Biosphere Zapovednik, Russian Far East, during the fall 2019 and fall 2020 over periods of 1–7 days. The different quantiles of displacement values are shown by line type. Shotin et al. (2022) found wild boar infected with African Swine Fever virus did not exhibit symptoms during the first three days after infection, and these displacements are shown in green. Four days since infection was the earliest wild boar showed symptoms, while 7 days since infection was the latest, and so displacement over these periods of time are shown in orange. Displacement values were calculated over 1–7 days for each successive day of available data from each individual wild boar.

far from the oak forests in which they were captured, with the greatest observed value of maximum displacement across individuals over a seven-day period (5.2 km) only 1.5 km greater than the maximum displacement traveled over 1 day (3.7 km). The displacement of wild boar in fall 2020 over this same period was much greater, especially at the upper quantiles of the distribution. Even in a period of 4 days – the minimum time until symptoms in ASF-infected pigs found by Shotin et al. (2022) – the 75th percentile of displacement was as great as 20.1 km, while the maximum displacement was 78.5 km, over 15 times greater than the year before. The maximum observed displacement increased marginally to 82.0 km when the period was increased to seven days, a much smaller increase than seen during the first three days.

Discussion

The outbreak of ASF across Eurasia has had serious ecological and economic consequences. Its main mechanisms of spread over large distances have been attributed to human transport (Guberti et al. 2022) because of the short distances wild boar most often travel in Europe (Prévot and Licoppe 2013, Podgórski and Śmietanka 2018, Taylor et al. 2020). Here, we provide an analysis of movement patterns of wild boar in a different ecological and human development context, namely the forests of the Russian Far East. Our findings indicate that wild boar movement behavior, resource availability, and the potential for spread of ASF into new areas are linked in a resource–movement–disease cascade.

The comparison with wild boar movement patterns living in Belgium demonstrates that wild boar in the Far East can travel larger distances than is typically observed in Europe:

our recording of 78.5 km straight-line distance traveled in just 4 days is remarkable. But such records are not novel. Several instances exist in the literature where wild boar travel similar or greater distances in Europe (Jerina et al. 2014, Miettinen et al. 2023, Popczyk et al. 2024). However, none of these studies reveal the mechanism for traveling such long distances. Here, we tried to illuminate the cause of the long-distance movements we observed, and directly related them to the risk of ASF spread.

Our results indicate that differences in wild boar movement behavior in the Far East between fall 2019 and fall 2020 were linked with the changing availability of mast resources between years and the spatial separation of specific mast-producing forests. In fall 2019, acorn production along the coast of the Zapovednik was high, three times higher than the average production of acorns over 38 years of sampling (unpubl.). Daily movements of our two GPS-collared wild boar were correspondingly low. They did not move far from their initial location of capture, and they concentrated use in a small home range within oak forests throughout the fall mast production period (and through the winter), as reflected by our fall 2019 RSF results. Bromley and Kucherenko (1983) similarly reported that in years of abundant acorns, wild boar often travel less than 1 km each day in the Russian Far East. This appears to be a common response to high availability of pulsed resources; similar behavior has been observed in Europe (Bisi et al. 2018) and the US among feral pigs (Singer et al. 1981).

However, when resources are scarce, wild boar can travel far in search of better fare. In fall 2020, acorn production was lower than average, with production only 30% from the year prior based on sampling plot counts. In Korean pine forests further inland, pine nut production was unremarkable.

Sampling counts of pine cones were 3 times greater than in 2019 (the worst year in 11 years of sampling), but still only 40% of the best year during that same period. We believe that the low production in acorns drove wild boar captured in oak forests near the coast in fall 2020 to search for pine nuts further inland. The quick transition from oak to pine forests along wild boar movement paths and their strong selection for pine forests in their areas of concentrated use support this hypothesis. This also aligns with claims by Bromley and Kucherenko (1983), who reported wild boar to travel up to 30–40 km each day, and even up to 300 km over two weeks in their search for pine nuts, especially in years of poor production.

Our moving-window analysis of the displacement of wild boar over the short incubation time of this isolate of ASF virus (ASFV/Primorsky 19/WB6723) indicates that infected wild boar can still travel great distances in only 3–7 days when pulsed resource availability is low. In fact, this is exactly what happened in the Russian Far East: the ASF outbreak in this region coincided with the period when wild boar were moving extensively in search of mast resources. While current guidelines for the management of ASF emphasize human sources of contagion, much remains unknown about ASF spread in east Asia, and the risk of spread among wild boar populations has likely been underestimated (Cadenas-Fernández et al. 2022). Past simulations have shown that habitat fragmentation can reduce the rate of spread of ASF (Dellicour et al. 2020, Salazar et al. 2022); indeed, our example data from Belgium come from highly fragmented habitats, and their distances traveled are correspondingly much less (Table 2). Similar patterns have been found in other, wide-ranging species: using the intensity of use metric, Mumme et al. (2023) found that elk *Cervus canadensis* and red deer *Cervus elaphus* use smaller areas more intensely in places with a greater human footprint. This follows global patterns in animal movement behavior: increased human footprint leads to decreased movement rates and scales (Tucker et al. 2018). But in the Russian Far East, managers face the inverse situation in which wild boar, searching for optimum resources, can easily travel great distances through contiguous forests (our study, Bromley and Kucherenko 1983), potentially carrying ASF with them. Other examples in Europe (Bisi et al. 2018) and southeast Asia exist where suids can move greater distances in response to varying mast availability (Luskin et al. 2017). In such places, we strongly encourage wildlife managers to consider the ecological context and resulting movement potential of wild suids to mitigate the spread of ASF into new areas.

The spread of highly contagious diseases can be heavily influenced by rare long-distance dispersal. Jeltsch et al. (1997) found that just one dispersal event per year can drive the spread of rabies among red fox *Vulpes vulpes*. Byrne et al. (2014) found that the potential dispersal distance of European badgers *Meles meles* was in fact much greater than previous studies had found based on restricted study areas, which helped explain the large-scale clustering of strains of bovine tuberculosis among setts. Licoppe et al. (2023) found that a rare 10 km movement of an ASF virus-infected wild boar in eastern Belgium in 2019 led to a new area becoming contaminated, even while the median rate of spread was below 2 km/month. Licoppe et al. (2023) used this maximum rate to establish ASF management zones accordingly. Similarly, we argue that when weighing the risks of ASF spread by wild boar, managers should consider the tail-end of movement distributions. We acknowledge that our data indicate wild boar typically do not travel far; the median displacement of wild boar after four days in fall 2020 was roughly 5 km (Table 2). But the tail-end of the displacement distribution tells a different story, with wild boar potentially traveling as far as 80 km by their fourth day since infection. Though relatively rare, these are exactly the kind of movements that influence the potential for disease dispersal. We recommend that efforts to model and management actions taken to control the spread of disease should place more importance on the tail-end of movement distributions.

In conclusion, our results demonstrate how contrasting movement responses to temporal and spatial variation in pulsed resource availability resulted in varying potentials for wild boar to spread ASF to new areas. With contiguous forest habitats across the Far East that pose no barriers to animal movement, this risk is heightened even further. We acknowledge that our sample size is small, and we are cautious to describe the behavior of a population based on results from just two individuals in fall 2019 and five individuals in fall 2020. But our observations of high densities of wild boar in 2019 in the oak forests, and the consistent, strong selection for Korean pine across collared individuals in 2020, the high level of connectivity among forest types across the Far East, and the agreement with past Russian observations suggest that long-distance movements may be common in an appropriate pulsed resource scenario. Despite management guidelines emanating out of Europe that minimize the role of wild suids in new outbreaks, we urge managers to reconsider the extent to which wild suids may drive long-distance spread of ASF and reflect this potential in predictive models and management decisions.

Author contributions

Scott Waller: Conceptualization (equal); Formal analysis (equal); Funding acquisition (supporting); Investigation

(equal); Methodology (equal); Project administration (supporting); Writing – original draft (equal); Writing – review and editing (equal). **Kevin Morelle**: Conceptualization (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Writing – original draft (equal); Writing – review and editing (equal). **Ivan Seryodkin**: Investigation (equal); Writing – review and editing (supporting). **Alexander Reebin**: Investigation (equal); Project administration (supporting). **Svetlana Soutyrina**: Investigation (supporting); Project administration (supporting); Writing – review and editing (supporting). **Alain Licoppe**: Investigation (equal); Writing – review and editing (supporting). **Mark Hebblewhite**: Formal analysis (supporting); Investigation (supporting); Methodology (supporting); Writing – review and editing (supporting). **Dale Miquelle**: Conceptualization (equal); Funding acquisition (lead); Investigation (equal); Methodology (supporting); Project administration (equal); Writing – review and editing (supporting).

Transparent peer review

The peer review history for this article is available at https://publons.com/publon/10.1002/wlb3.01276.

Data availability statement

Our data comes from a Russian federal reserve, and we cannot make it publicly available. Data may be made available upon request to the corresponding author.

Supporting information

The Supporting information associated with this article is available with the online version.

References

Almeida, P. J. A. L., Vieira, M. V., Kajin, M., Forero-Medina, G. and Cerqueira, R. 2010. Indices of movement behaviour: conceptual background, effects of scale and location errors. – Zoologica 27: 674–680.

Altizer, S., Bartel, R. and Han, B. A. 2011. Animal migration and infectious disease risk. – Science 331: 296–302.

Bisi, F., Chirichella, R., Chianucci, F., Von Hardenberg, J., Cutini, A., Martinoli, A. and Apollonio, M. 2018. Climate, tree masting and spatial behaviour in wild boar (*Sus scrofa* L.): insight from a long-term study. – Ann. For. Sci. 75: 46.

Boyce, M. S., Vernier, P. R., Nielsen, S. E. and Schmiegelow, F. K. A. 2002. Evaluating resource selection functions. – Ecol. Model. 157: 281–300.

Bromley, G. F. and Kucherenko, S. P. 1983. Ungulates of the southern Far East USSR. – Nauka Press.

Bürkner, P. C. 2017. *brms*: an R package for Bayesian multilevel models using Stan. – J. Stat. Softw. 80.

Byrne, A. W., Quinn, J. L., O'Keeffe, J. J., Green, S., Paddy Sleeman, D., Wayne Martin, S. and Davenport, J. 2014. Large-scale movements in European badgers: Has the tail of the movement kernel been underestimated? – J. Anim. Ecol. 83: 991–1001.

Cadenas-Fernández, E., Ito, S., Aguilar-Vega, C., Sánchez-Vizcaíno, J. M. and Bosch, J. 2022. The role of the wild boar spreading African swine fever virus in Asia: another underestimated problem. – Frontiers Vet. Sci. 9: 1–7.

Dellicour, S., Desmecht, D., Paternostre, J., Malengreaux, C., Licoppe, A., Gilbert, M. and Linden, A. 2020. Unravelling the dispersal dynamics and ecological drivers of the African swine fever outbreak in Belgium. – J. Appl. Ecol. 57: 1619–1629.

Denstedt, E. et al. 2021. Detection of African swine fever virus in free-ranging wild boar in Southeast Asia. – Transbound. Emerg. Dis. 68: 2669–2675.

Dougherty, E. R., Seidel, D. P., Carlson, C. J., Spiegel, O. and Getz, W. M. 2018. Going through the motions: incorporating movement analyses into disease research. – Blackwell Publishing Ltd.

European Food Safety Authority (EFSA) et al. 2018. Epidemiological analyses of African swine fever in the European Union (November 2017 until November 2018). – E.F.S.A. J. 16.

Fieberg, J., Signer, J., Smith, B. and Avgar, T. 2021. A 'How to' guide for interpreting parameters in habitat-selection analyses. – J. Anim. Ecol. 90: 1027–1043.

Fithian, W. and Hastie, T. 2013. Finite-sample equivalence in statistical models for presence-only data. – Ann. Appl. Stat. 7: 1917–1939.

Gillies, C. S., Hebblewhite, M., Nielsen, S. E., Krawchuk, M. A., Aldridge, C. L., Frair, J. L., Saher, D. J., Stevens, C. E. and Jerde, C. L. 2006. Application of random effects to the study of resource selection by animals. – J. Anim. Ecol. 75: 887–898.

Guberti, V., Khomenko, S., Masiulis, M. and Kerba, S. 2022. African swine fever in wild boar ecology and biosecurity, 2nd edn. – World Organization for Animal Health and European Commission.

Hayward, M. W., Jędrzejewski, W. and Jędrzejewska, B. 2012. Prey preferences of the tiger *Panthera tigris*. – J. Zool. 286: 221–231.

Heptner, V. G., Nasimovich, A. A. and Bannikov, A. G. 1988. Mammals of the Soviet Union, Vol 1. – Smithsonian Inst..

Hooten, M. B., Johnson, D. S., McClintock, B. T. and Morales, J. M. 2017. Animal movement. – CRC Press.

Hosmer, D. and Lemeshow, S. 2000. Applied logistic regression, 1st edn. – John Wiley & Sons.

Jeltsch, F., Mu, M. S., Grimm, V., Wissel, C. and Brandl, R. 1997. Pattern formation triggered by rare events: lessons from the spread of rabies. – Proc. R. Soc. B 264: 495–503.

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

Krestov, P. V. 2003. Forest vegetation of Easternmost Russia (Russian Far East). Page. – In: Kolbek, J., Šrůtek, M. and Box, E. O. (eds), Forest vegetation of NorthEast Asia. Springer.

Licoppe, A., De Waele, V., Malengreaux, C., Paternostre, J., Van Goethem, A., Desmecht, D., Herman, M. and Linden, A. 2023. Management of a focal introduction of ASF virus in wild boar: the Belgian experience. – Pathogens 12.

Loretto, D. and Vieira, M. V. 2005. The effects of reproductive and climatic seasons on movements in the black-eared opossum (*Didelphis aurita* Wied-Neuwied, 1826). – J. Mammal. 86: 287–293.

Luskin, M. S., Meijaard, E., Sheherazade, S., Walzer, C., Linkie, M., Futures, B., Begawan, S. and Darussalam, B. 2020. African Swine Fever threatens Southeast Asia's endemic wild pig species. – Conserv. Lett. 14: 1–11.

Manly, B. F. J., McDonald, L. L., Thomas, D. L., McDonald, t. L. and Erickson, W. P. 2002. Resource selection by animals. – Springer.

Miettinen, E., Melin, M., Holmala, K., Meller, A., Väänänen, V.-M., Huitu, O. and Kunnasranta, M. 2023. Home ranges and movement patterns of wild boars (*Sus scrofa*) at the northern edge of the species' distribution range. – Mamm. Res. 68: 611–623.

Morelle, K. 2015. Wild boar movement ecology across scales: insights from a population expanding into agroecosystems of Southern Belgium. – Université de Liège – Gembloux Agro-Bio Tech.

Morelle, K., Podgórski, T., Prévot, C., Keuling, O., Lehaire, F. and Lejeune, P. 2015. Towards understanding wild boar *Sus scrofa* movement: a synthetic movement ecology approach. – Blackwell Publishing Ltd.

Morelle, K., Bubnicki, J., Churski, M., Gryz, J., Podgórski, T. and Kuijper, D. P. J. 2020. Disease-induced mortality outweighs hunting in causing wild boar population crash after African swine fever outbreak. – Front. Vet. Sci. 7.

Morelle, K., Barasona, J. A., Bosch, J., Heine, G., Daim, A., Arnold, J., Bauch, T., Kosowska, A., Cadenas-Fernández, E., Aviles, M. M., Zuñiga, D., Wikelski, M., Vizcaino-Sanchez, J. M. and Safi, K. 2023. Accelerometer-based detection of African swine fever infection in wild boar. – Proc. R. Soc. B. 290: 20231396.

Muff, S., Signer, J. and Fieberg, J. 2020. Accounting for individual-specific variation in habitat-selection studies: efficient estimation of mixed-effects models using Bayesian or frequentist computation. – J. Anim. Ecol. 89: 80–92.

Mumme, S. et al. 2023. Wherever I may roam – human activity alters movements of red deer (*Cervus elaphus*) and elk (*Cervus canadensis*) across two continents. – Global Change Biol. 29: 5788–5801.

Noonan, M. J., Fleming, C. H., Akre, T. S., Drescher-Lehman, J., Gurarie, E., Harrison, A. L., Kays, R. and Calabrese, J. M. 2019. Scale-insensitive estimation of speed and distance travelled from animal tracking data. – Movem. Ecol. 7: 1–15.

O'Neill, X., White, A., Ruiz-Fons, F. and Gortázar, C. 2020. Modelling the transmission and persistence of African swine fever in wild boar in contrasting European scenarios. – Sci. Rep. 10.

OIE. 2020. African swine fever (ASF) Report– N° 54: September 18 to October 1, 2020, https://www.woah.org/app/uploads/2021/03/report-54-current-situation-of-asf.pdf.

Pepin, K. M., Brown, V. R., Yang, A., Beasley, J. C., Boughton, R., VerCauteren, K. C., Miller, R. S. and Bevins, S. N. 2022. Optimising response to an introduction of African swine fever in wild pigs. – Transbound. Emerg. Dis. 69: e3111–e3127.

Podgórski, T. and Śmietanka, K. 2018. Do wild boar movements drive the spread of African Swine Fever? – Transbound. Emerg. Dis. 65: 1588–1596.

Popczyk, B., Klich, D., Nasiadka, P., Nieszała, A., Gadkowski, K., Sobczuk, M., Balcerak, M., Kociuba, P., Olech, W. and Purski, L. 2024. Over 300 km dispersion of wild boar during hot summer, from Central Poland to Ukraine. – Animals 14.

Posit team. 2023. RStudio: integrated development environment for R. Posit software. – PBC.

Prévot, C. and Licoppe, A. 2013. Comparing red deer (*Cervus elaphus* L.) and wild boar (*Sus scrofa* L.) dispersal patterns in southern Belgium. – Eur. J. Wildl. Res. 59: 795–803.

Salazar, L. G., Rose, N., Hayes, B., Hammami, P., Baubet, E., Desvaux, S. and Andraud, M. 2022. Effects of habitat fragmentation and hunting activities on African swine fever dynamics among wild boar populations. – Preventive Vet. Med. 208: 1–11.

Sauter-Louis, C., Schulz, K., Richter, M., Staubach, C., Mettenleiter, T. C. and Conraths, F. J. 2022. African swine fever: why the situation in Germany is not comparable to that in the Czech Republic or Belgium. – Transbound. Emerg. Dis. 69: 2201–2208.

Schielzeth, H. and Forstmeier, W. 2009. Conclusions beyond support: overconfident estimates in mixed models. – Behav. Ecol. 20: 416–420.

Schwalb-Willmann, J., Remelgado, R., Safi, K. and Wegmann, M. 2020. moveVis: Animating movement trajectories in synchronicity with static or temporally dynamic environmental data in r. – Methods Ecol. Evol. 11: 664–669.

Shotin, A. R., Igolkin, A. S., Ali, M., Shevchenko, I. V., Bardina, N. S., Morozova, E. O. and Shevtsov, A. A. 2022. African swine fever in the Primorsky Krai: disease situation and molecular and biological properties of the isolate recovered from a wild boar long bone. – Vet. Sci. Today 11: 347–358.

Signer, J., Fieberg, J. and Avgar, T. 2019. Animal movement tools (amt): R package for managing tracking data and conducting habitat selection analyses. – Ecol. Evol. 2019: 880–890.

Singer, F. J., Otto, D. K., Tipton, A. R. and Hable, C. P. 1981. Home ranges, movements, and habitat use of European wild boar in Tennessee. – J. Wildl. Manage. 45: 343–353.

Taylor, R. A., Podgórski, T., Simons, R. R. L., Ip, S., Gale, P., Kelly, L. A., Snary, E. L. and Taylor, C. A. R. 2020. Predicting spread and effective control measures for African swine fever-Should we blame the boars? – Transbound. Emerg. Dis. 68: 397–416.

Tucker, M. A. et al. 2018. Moving in the Anthropocene: global reductions in terrestrial mammalian movements Downloaded from. – Page Science.

Vehtarh, A., Gelman, A., Simpson, D., Carpenter, B. and Burkner, P. C. 2021. Rank-normalization, folding, and localization: an improved (Formula presented) for assessing convergence of MCMC (with discussion). – Bayesian Anal. 16: 667–718.

Waller, S. J., Brodie, J., Hebblewhite, M., Robinson, H. and Miquelle, D. 2022. Evaluating the use of camera traps to monitor ungulate prey in the Russian Far East. – Master's thesis, Univ. of Montana, USA.

Wilber, M. Q., Yang, A., Boughton, R., Manlove, K. R., Miller, R. S., Pepin, K. M. and Wittemyer, G. 2022. A model for leveraging animal movement to understand spatio-temporal disease dynamics. – Ecol. Lett. 25: 1290–1304.

Zakharova, O. I., Titov, I. A., Gogin, A. E., Sevskikh, T. A., Korennoy, F. I., Kolbasov, D. V., Abrahamyan, L. and Blokhin, A. A. 2021. African swine fever in the Russian Far East (2019–2020): spatio-temporal analysis and implications for wild ungulates. – Front. Vet. Sci. 8.