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ORIGINAL PAPER

Home ranges and movement patterns of wild boars (*Sus scrofa*) at the northern edge of the species' distribution range

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Abstract

In Finland, the wild boar (Sus scrofa L.) lives on the northernmost edge of the species' distribution range, and the population mainly originates from individuals immigrating from Russia. Most of the current population lives in the southeastern part of the country, and the wild boar is steadily expanding further. To develop effective risk and population management in novel northern wild boar regions, detailed information about the species' local ecology is required. To estimate wild boar movement patterns, 17 adult wild boars were monitored using GPS collars from May 2020 to September 2022 in the core region of the current distribution. The average total home ranges of wild boars (87.1 ± 17 km2 MCP, 33 ± 5.5 SE km2 95% KDE) were larger compared with studies from southern latitudes. The length of nocturnal activity times varied seasonally. All studied individuals at the border zone (N = 15) showed continuous transboundary movements, with home range core areas located mainly on the Russian side. Wild boar locations were predominantly in the Russia border zone, especially resting sites during the daytime. Most locations in Finland were from night-time feeding excursions. Our study shows that, although home ranges are large, adult wild boars are relatively sedentary also in northern latitudes. However, the movement capacity of the species enables the transboundary spread of diseases such as African swine fever. Our results provide information for risk management and emphasize the importance of transboundary collaboration in the monitoring and management of common wild boar populations.

Keywords ASF · GPS collar · Spatial ecology · Activity · Transboundary movement

Introduction

The wild boar (*Sus scrofa* L.) is one of the most common native ungulates in Europe (Barrios-Garcia and Ballari 2012). Over the past decades, wild boars have expanded their range throughout the continent (Sáez-Royuela and Tellería 1986; Danilov and Panchenko 2012; Massei et al. 2015). Range expansion has also happened at the northernmost edge of the species' distribution area in Finland (Kukko et al. 2018). The current Finnish wild boar population mostly originates from individuals immigrating over the southeastern border from Russia and, to some degree, from individuals escaping from enclosures on both sides of the border (Danilov and Panchenko 2012; Kukko et al. 2018; Markov et al. 2022). Wild boars belonged to the native fauna of present-day Finland some 8000 years ago but disappeared due to unfavorable climatic conditions and prehistoric hunting pressure (Ukkonen et al. 2015). The first contemporary observations of single free-ranging wild boars were made in the 1950s (Ermala 1996). From the 1970s onwards, the

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population has slowly re-established as part of the Finnish fauna and has lately increased in numbers (Erkinaro et al. 1982; Sáez-Royuela and Tellería 1986; Kukko et al. 2018). Climate change-driven milder winters with less snow and ground frost have enhanced the species´ expansion northwards (Melis et al. 2006; Markov et al. 2019). Nowadays, supplementary feeding is presumed to promote the survival of wild boars during harsh winters (Oja et al. 2014; Markov et al. 2022). According to the latest estimates, the Finnish wild boar population stands at ca. 3100 individuals (median with 90% probability interval: 2161–4560; Ruha and Kunnasranta 2022). The main distribution area is in the southeastern part of the country (regions of South Karelia, Kymenlaakso, and eastern Uusimaa), but sounders including piglets have been observed and shot as far north as ca. 63.8°N. Single individuals have been observed even further north, up to 65°N (Kukko et al. 2018).

Wild boars are one of the most widely distributed ungulates in the world due to their high reproductive rate, adaptability, and opportunistic feeding habits. Especially at high densities, wild boar populations facilitate pathogen transmission, damage agriculture, and precipitate traffic accidents, while their effects to biodiversity may also be positive through ecosystem engineering and predator–prey interactions (e.g., Barrios-Garcia and Ballari 2012; Abrantes and Vieira-Pinto 2023). In novel regions, like Finland, this naturally expanding immigrant species can provide hunting opportunities on the one hand but elevated human–wild boar conflicts, like crop damages, on the other (Miettinen et al. 2022). The most acute economic threat is the species´ potential contribution to the introduction, persistence, and spread of African swine fever (ASF), a high-mortality viral disease of porcine species. Contrary to many European countries, Finland has thus far remained ASF-free (Cwynar et al. 2019) despite being identified as one of the countries with the highest risk of ASF introduction (De la Torre et al. 2015; Kyyrö et al. 2017).

The effects and risks posed by expanding wild boar populations are essentially linked to the space use and movement of the species. Wild boars are known to exhibit behavioral plasticity and capacity to adjust its spatiotemporal behavior in response to factors such as population demography, climatic conditions, resource availability, predation, and hunting pressure (Podgórski et al. 2013; Morelle et al. 2015; Brivio et al. 2017; Garza et al. 2018; Clontz et al. 2022). Human disturbance, season, and wild boar density together with the distribution and abundance of foraging sites and resting sites are known to affect the home range sizes and habitat selection of the species (Meriggi and Sacchi 2001; Fattebert et al. 2017; Ciach et al. 2022). In studies using the most comparable methods, mean wild boar home ranges have varied between 4 and 11 km^2 in 95% kernel density estimation (Fattebert et al. 2017; Froehly et al. 2020; Gaudiano et al. 2022) and 21–52 km^2 in minimum convex polygon estimation (Adkins and Harveson 2007; Schlichting et al. 2016; Peris et al. 2020). Wild boar movement is restricted to the night hours, at least in areas with human disturbance and hunting (Russo et al. 1997; Keuling et al. 2008a). In addition, the duration and peaks of daily activity are known to fluctuate with environmental and seasonal conditions (Lemel et al. 2003; Jánoska et al. 2018; Johann et al. 2020). However, most studies on the movement ecology of wild boars have only been carried out in southern latitudes.

In general, wild boar studies from the northernmost regions are scarce and mostly focus on distribution (Erkinaro et al. 1982; Kukko et al. 2018) and agricultural damage (Miettinen et al. 2022), while their movement ecology has not been studied before. To this end, information on wild boars at the northern edge of their range, in distinctly seasonal boreal environments, is sorely needed to facilitate effective population management, especially if ASF spreads to Finland and other Nordic countries. The main objective of this study was to explore the home range size, seasonal circadian activity, and monthly circadian movement patterns of northern wild boars in comparison with earlier findings from southern populations. In addition, we aimed to examine the movement patterns of wild boars in relation to the Finnish–Russian border zone. To achieve these objectives, we fitted GPS tracking collars on free-ranging wild boars. We hypothesized that (1) home ranges of the studied wild boars are larger compared with southern studies due to the lower density of resources and conspecifics, (2) movement and activity peak at night times and during seasons of increased resources, and (3) differences in resources and disturbance between the two sides of the border result in active transboundary movement. Based on these results, we considered the implications for population management and risk mitigation.

Material and methods

Study areas and live capturing

Live-trap capturing and GPS tagging of free-ranging wild boars was conducted in two study areas in the main distribution area of the Finnish wild boar population in southeastern Finland (60°N, 27°E, Fig. 1) from April 2020 to September 2022. The climate in the study areas belongs to the southern boreal temperate zone, with mean annual precipitation of 600–700 mm and mean annual temperature of + 4–5 °C. The average snow cover duration is around 115–130 days per year, and the snow depth in March is 40–50 cm during average winters (Kersalo and Pirinen 2009). The region is characterized by vegetation consisting mainly of mixed coniferous forests (Scots pine *Pinus sylvestris* L., Norway

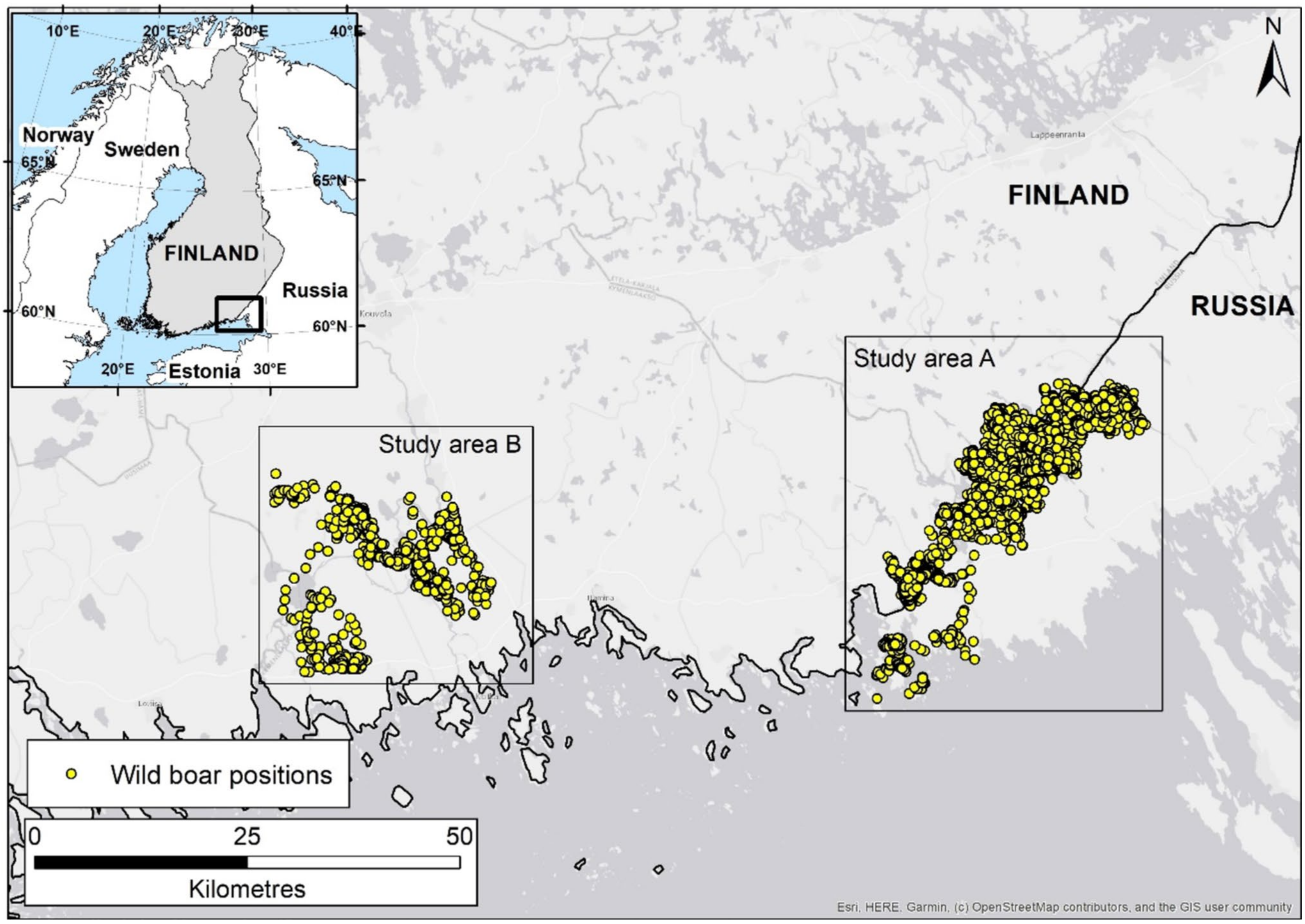

Fig. 1 Location of the study areas and GPS locations of tracked wild boars ($N = 17$, two in study area B and 15 in study area A)

spruce *Picea abies* (L.) L.H.Karst) with deciduous species (birches *Betula* spp., alders *Alnus* spp., and European aspen *Populus tremula* L.) present in minority. The area also has features such as bogs and farmlands. Most of the landscape is used for agriculture, and most of the forests are actively managed. Numerous supplemental feeding sites for game animals, such as wild boars, were located within the study areas. Supplemental feeding of wild boar is not regulated by national legislation but is recommended for hunting purposes only (Markov et al. 2022).

Wild boar densities in the study region are estimated at approximately 2–3 individuals/10 km^2 (Ruha and Kunnasranta 2022). The exact capture sites in the border study area (Fig. 1, area A) were located on the Finnish side of the Finnish–Russian border zone, 0.1–2.8 km from the border. The landscape on the Russian side of the border zone is dominated by continuous, less-managed, mature mixed boreal forests, whereas the mostly coniferous commercial forests on the Finnish side occur in smaller patches (Muukkonen et al. 2009). Based on satellite images of our study sites, modern agricultural fields are more abundant in Finland while bogs are more abundant in Russia. In Finland, the border zone is narrow (0.1–3 km) and allows licensed civilian movement and land use (Finlex 416/2022), whereas human activity is strictly restricted in the Russian border zone, which is several times wider (Law of the Russian Federation 4730). The capture site in the interior study area (Fig. 1, area B) was located around 60 km west from the border zone. Compared with the border study area, the interior area has more farmlands, but the structure of forest is similar throughout southern Finland.

Wild boars were live-captured using square-shaped box traps (2.5 m × 2.5 m) constructed from 12-mm thick and 1.25-m high plywood boards, supported with 2″ by 4″ inch sawn planks. These traps were equipped with 90-cm wide guillotine-style single-catch plywood doors. Plywood corral traps (25 m^2) with saloon doors were also used. For preventing captured animals from jumping/climbing out of the traps, inwards inclined corner guards (40-cm wide plywood boards) were installed. Traps were baited, mostly with maize and oats, and placed at supplementary feeding sites, other known foraging locations, or trails commonly used by wild boars. The traps were kept set between dusk and dawn. Doors were triggered by wild boars activating a tripwire or with custom-made PMR-based remote triggering. All traps were monitored with remote game cameras (Uovison UM595-3G) and remote-triggered traps fitted with custom-made real-time cameras (Nedis video doorbell). A closing trap door activated the live trap alarm (Keep Guard KG45), which sent an alarm message to the research team via mobile phone.

Immobilization and tagging

Wild boars were immobilized for tagging using a combination of medetomidine (30 mg/ml, target dose 0.11 mg/kg), a mixture of zolazepam and tiletamine (Zoletil® 250 mg/ml, target dose 3.75 mg/kg), and ketamine (Ketaminol® 100 mg/ml, target dose 1.5 mg/kg). This multimodal anesthesia approach was chosen because it allows using lower doses of each drug than when a single-agent approach is used, decreases the induction time, increases the likelihood of reaching the required level of sedation and immobilization, improves recovery, and decreases the likelihood of undesirable side effects (Kreeger and Arnemo 2012). The anesthesia was designed by a veterinarian. The dose of the anesthetic mixture was calibrated after visually estimating the body weights of the captured animals. A combination of these drugs was dart-injected intramuscularly into the large muscle mass of the hindquarters with 3-ml blowpipe syringes and barbet 40-mm needles with an internal diameter of 2 mm using an injection pistol (RD406, TeleDart).

Animals were blindfolded during handling, and their welfare was continuously monitored by measuring oxygen saturation and heart rate using a portable veterinary pulse oximeter (VE-H100B) and by measuring rectal body temperature (normal temperature 37.0 to 39.5 °C). If needed, body temperature was lowered or increased manually with water or a space blanket. All handled animals were given 100% oxygen to breathe via a nasal tube to maintain normal arterial oxygen saturation. While under anesthesia, the animals were weighed, measured, and aged. Age was assessed by examining the eruption stage of the molars and premolars (Matschke 1967), and individuals were classified into juveniles (< 12 months), subadults (12–24 months), and adults (> 24 months). One to two individuals were handled simultaneously. Uniquely identifiable ear tags (Combi 3000 Små, Stallmästaren, Sweden) were placed in both ears of all handled individuals. Due to potential drug residues, the tagging date was marked into the ear tags to prevent human consumption of the meat for 6 months, as required by the Finnish Medicines Agency Fimea.

The wild boars were allowed to recover in the trap after sedation reversal of medetomidine by atipamezole (Antisedan® 5 mg/ml, target dose 0.3–0.5 mg/kg). Animals were monitored until they were mobile and then released at the trapping site. The long-term welfare of collared animals was monitored by game camera traps located at supplementary feeding sites and along regularly used wild boar trails of the study area.

Wild boars with a body weight of over 60 kg ($N = 18$, Supplement 1) were equipped with GPS collars (VECTRONIC GPS PLUS, weight approximately 1.5 kg). The collars were programmed to record GPS locations at 1-h intervals, and they were equipped with a mortality sensor that reported if the animal had been motionless for 24 h. The collars were also pre-programmed to automatically drop off after a tracking period of 80 weeks in case the connection to a collar was lost (the drop-off unit is independent of the GPS unit). During the study, five collars dropped off due to a loose attachment, and two animals were shot by hunters. One of the shot individuals had a superficial skin lesion in the neck area apparently caused by an excessively tight collar. Subsequently, all collars were intentionally released earlier via the satellite-based drop-off system to prevent weight gain-related skin abrasions. During the approximated weight-gaining season (June–November), the drop-off was employed after approximately three tracking months (10 collars). Two collars malfunctioned while attached to the animal, so that no signals were sent to nor received by the collar.

Home range, activity, and movement estimation

Locations from the first 2 days of active GPS tracking were omitted from the activity, movement, and home range size analyses, as the animals may exhibit anomalous behavior after sedation. Unreliable GPS locations were also removed from the data based on the position dilution of precision (PDOP, 2-D > 5, and 3D > 10; Lewis et al. 2007). Fix success rates of GPS collars were calculated as the proportion of received reliable fixes from the expected number of fixes (24 fixes/day). Spatial analyses were carried out on data from those study animals that had at least 500 GPS fixes each ($N = 17$, Supplement 1). This limit was chosen based on the flattening curve of an average home range size of around 400 and 500 fixes (Fig. 2). This limit translates to a minimum of ca. 20 tracking days.

The home ranges of individual wild boars were calculated utilizing two methods: minimum convex polygon (100% MCP) and fixed kernel density estimation (95% and 50% KDE) using the Ranges 9 software (Kenward et al. 2014). The MCP and KDE approaches were chosen because they are the most typically used contouring methods in recent spatial ecology studies of wild boars (Bisi et al. 2018; Garza et al. 2018; Jánoska et al. 2018; Podgórski and Śmietanka 2018; Clontz et al. 2022; Gaudiano et al. 2022). The KDE approach is especially recommended for improving the

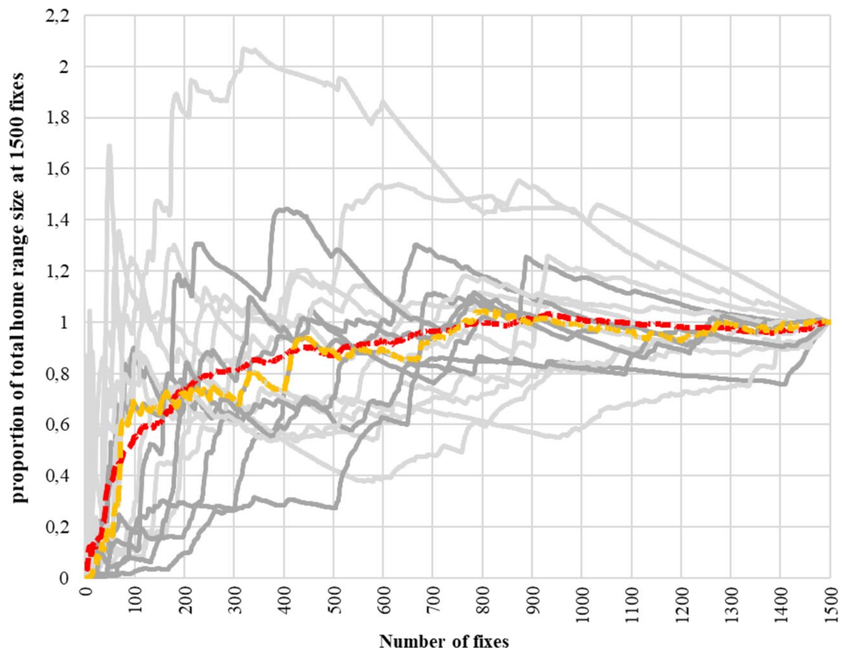

Fig. 2 Incremental accumulation of wild boar home range sizes (95% kernel density estimation). Individual animal data in solid gray lines (light: females, dark: males). For conciseness, the number of fixes is restricted to 1500 (approximately two tracking months), as home range is expected to settle within that time. Average home range accumulation in the red dashed line and median accumulation in the orange dashed line. The curve of both average and median accumulation reaches 0.9 and flattens around 400–500 fixes

comparability of results between studies (Peris et al. 2020). The MCP approach typically overestimates home range size by including all location points and unvisited areas between them as part of the home range. It is also important to note that tracking data are inherently autocorrelated, which is not accounted for by either of the chosen methods (Fleming et al. 2015, 2022).

To define the total home range size, 95% kernel estimates (KDE95) were constructed, and 50% (KDE50) was used to define the core areas, utilizing an ad hoc smoothing parameter ($h_{ad\ hoc}$) following Kie (2013). This (1) limits fragmentation of the total home range contour, which often occurs with approaches like least square cross validation (h_{lscv}) and (2) avoids overestimation of the home range in cases when an animal's location point density does not follow a normal distribution as expected when using the reference bandwidth (h_{ref}) only (Walter et al. 2011; Kie 2013). The applied $h_{ad\ hoc}$ was established by reducing the h_{ref} multiplier in 0.1 increments (0.9 h_{ref}, 0.8 h_{ref}, …0.1 h_{ref}). This reduction was continued to the smallest multiplier that still maintained a non-fragmented contour in KDE95. If the contour was fragmented already in h_{ref}, the result was accepted as such ($h_{ad\ hoc} = h_{ref}$). With each study animal, KDE50 was calculated with the same smoothing parameter as KDE95.

The activity status of an animal (sedentary or active) was deduced from moving distances and location accuracy. To measure the GPS inaccuracy in the normal habitats of our study animals, we analyzed data from six stationary collars at their drop-off sites. The mean distance that encapsulates 95% of all false movement of the collar (i.e., location inaccuracy) was 50 m. Therefore, all study animal movements of less than 50 m between consecutive hours were classified as sedentary, and higher values were considered active. Although we are unable to detect small-scale movement (for example, switching resting spots or foraging at point food sources) with this approach, activity can be monitored at a broader scale. The seasonal circadian probability of activity was analyzed using a generalized additive mixed model (GAMM) with binomial distribution and the logit-link function. In the model, the explanatory factors for the activity status were season, sex, and the interaction between local standard time (LST) and season. Study animal individuals were included as random factor. The GAMM was fitted using the REML method.

The mean daily movement of wild boars was calculated by measuring the sum of Euclidean distances between consecutive GPS locations within 24 h. Monthly circadian movement rhythms were examined by measuring distances between consecutive hours. The mean distance (m) traveled by the studied animals in a 60-min period was calculated for each day, and this was later analyzed on a monthly basis. An individual was included in the monthly mean calculations only if its tracking period for the given month exceeded 2 weeks.

GPS locations, home ranges, and border effects were examined and mapped with QGIS (v3.26.0; QGIS Development Team 2022). Activity and movement pattern examination and statistical tests were performed with R (v4.0.4; R Core Team 2021) and the activity GAMM with R package mgcv (Wood 2017). The Wilcoxon rank sum test was used to analyze intrasexual differences.

Results

We received a total of 29 295 (mean = 1 627, range = 264–3787; Supplement 1) locations from the 18 wild boars. The average fix success rate of the GPS collars was 85%, and the average tracking period of wild boars used in the home range analyses ($n = 17$) was 87 days (42–221). Maximum observed distances from an individual to its capture site ranged from 4 to 27 km. All but two individuals (BLA22 and BlI22) were captured in the border study area.

Home range sizes

The mean home range according to MCP analysis was 87.1 (± 17 SE) km^2. Male ($N = 7$) home ranges were larger (122.3 ± 25.5) than those of females ($N = 10$, 62.5 ± 20.1; W = 59, $P = 0.019$). The same pattern occurs with KDE95-based estimates of home range sizes, with a mean of 33 (± 5.5 SE) km^2 (males: 48.5 ± 8.6; females: 23.3 ± 5.2; W = 58, $P = 0.025$). Mean (± SE) core area (KDE50) size was 7.8 (± 1.3) km^2, with male core areas (10.4 ± 1.9) tending to exceed those of females (6.0 ± 1.5), but not significantly (W = 52, $P = 0.109$). Two of the studied individuals (WEN21 and BLI22) had multiple long-distance movements during the tracking period, which resulted in notably larger home range estimates. Both studied animals (BLA22 and BLI22) in the interior study area had larger home ranges than individuals in the border area (Supplement 1).

The mean kernel smoothing parameter value (h) was 61.6. With most of the individuals, KDE estimations used h_{ref} due to fragmentation of the contours, while the reduced $h_{ad\ hoc}$ was used for four studied animals (three $0.8h_{ref}$ and one $0.7h_{ref}$). The mean change in area from h_{ref} to $h_{ad\ hoc}$ was − 4.1 km^2 (± 1.5 SE) in KDE95 and − 1.3 km^2 (± 0.4 SE) in KDE50.

Activity and movement patterns

Wild boars were mainly nocturnal, with the highest probability of activity and hourly movements occurring in the twilight hours (Fig. 3). Throughout the year, activity peaks during or shortly after sunset. Seasonal differences (Fig. 3A; Supplement 2) occur mainly in the length of activity time: In winter and spring, activity decreases shortly after the peak reaching the lowest probability of activity in the morning hours, whereas in summer and autumn, activity is maintained longer and decreases slowly to its lowest point in the late afternoon. On average, study animals were active for ca. 50% of any 24-h period. The observed times of activity were the highest in summer and autumn (up to 59% in August). Individuals tracked during winter spent most of their time sedentary, with the average time on the move being below 40% (down to 21% in February). When comparing sexes during the months with the most data, females spent more time being mobile in the summer (June–August) and males in early winter (November–December). However, the effect of sex was non-significant to the overall probability of activity (GAMM, $\chi^2 = 1.55$, $P = 0.213$; Supplement 2).

The mean daily movement of the studied animals was 5.4 (± 0.3 SE) km. Following the pattern in home range sizes, the highest daily means were made by males (up to 7.5 km; mean = 5.9 ± 0.5), but the difference with females was not significant (5.0 ± 0.3; W = 47, $P = 0.261$). As with the activity time, monthly circadian movement patterns show clear seasonal differences (Fig. 3B): In the winter months, when activity is reduced, the average movement distances are short even during the most active hours, whereas the distances show clearer circadian patterns from June to October (though the data are insufficient for a proper analysis of monthly differences). Of the months with data from both sexes, differences based on visual comparisons are most notable in June–July, when males move longer distances during the nights and hardly any in the afternoons, while females maintain some movement uniformly around the clock.

Transboundary movements

The home ranges, particularly the core areas, of wild boars ($N = 15$) in the border study area were mostly located on the Russian side of the border (Fig. 4). On average, 76% (43.7–99.7%) of wild boar locations in this study area were on the Russian side of the border. This pattern was most prominent during daytime, as most locations on the Finnish side were from night-time. Wild boars were mobile for 58% of the hours spent in Finland, whereas active movement was reduced to 43% of the time while in Russia. On the Finnish side, location fixes are largely from supplemental feeding sites and crop fields.

Discussion

This study is the first publication to report on the home ranges, activity, and movement patterns of wild boars at their northernmost distribution range in eastern Fennoscandia. The average total home ranges of wild boars were approximately 87 km^2 by MCP100 and 33 km^2 by KDE95. The individuals at the Finnish–Russian border zone showed continuous transboundary movements, with

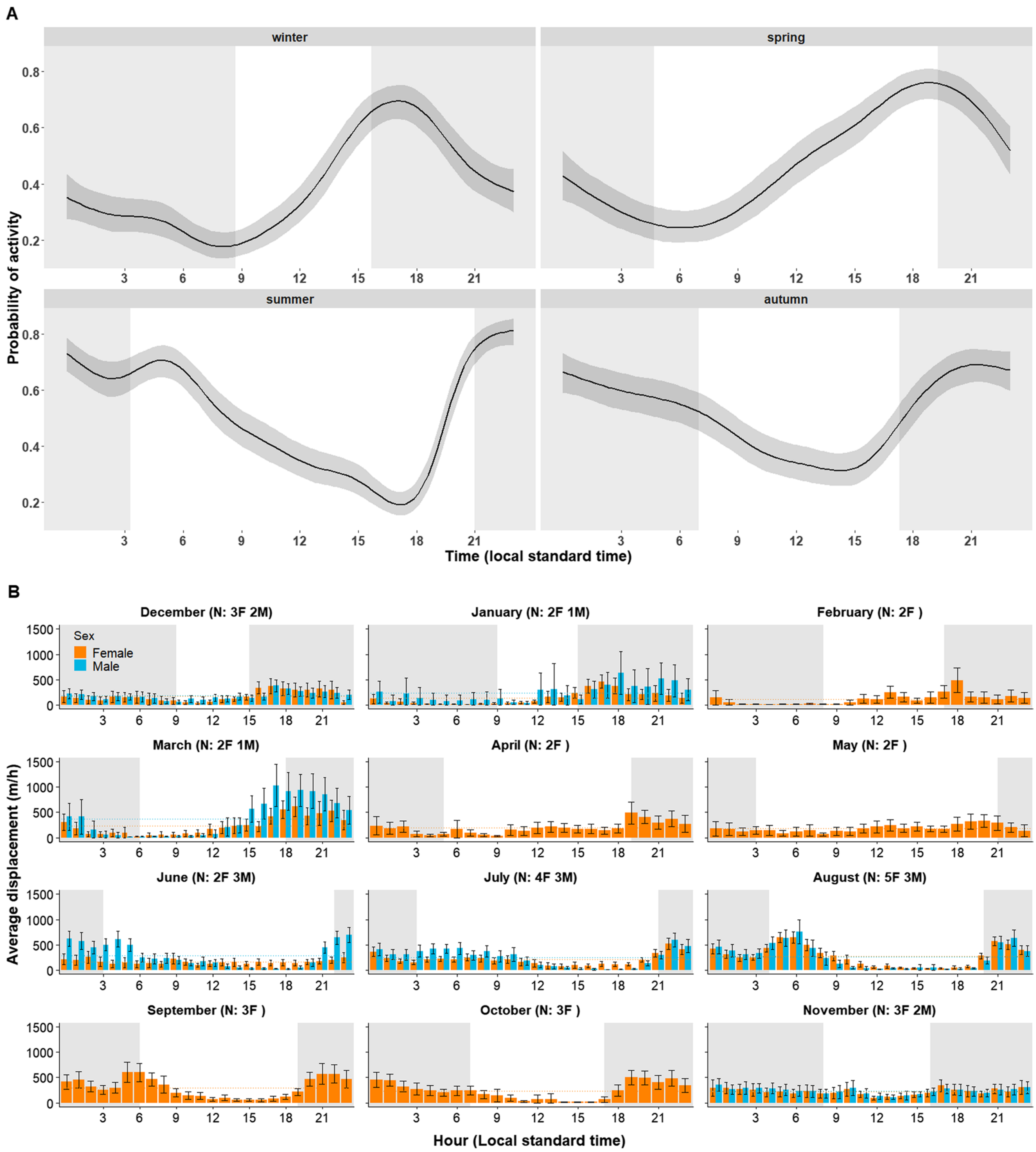

Fig. 3 **A** Seasonal circadian probability of activity (over 50 m of movement) and 95% confidence intervals of 17 GPS-tagged wild boar individuals. Mid-season daylight hours represented as white background. **B** Monthly circadian movement patterns based on an average hourly Euclidean displacement and 95% confidence intervals. Female data are shown in orange and male data in blue (number of individuals given in the titles). Daily mean distances are shown as horizontal lines. Only individuals with ≥ 2 weeks of monthly data are included in the graph. Monthly average daylight hours represented as white background

daytime resting predominantly on the Russian side and visits to Finland mainly during active nocturnal hours. These findings provide new information on wild boar spatial ecology that can be of high value for the future management of this novel species, especially when assessing the risk of disease spread into new areas.

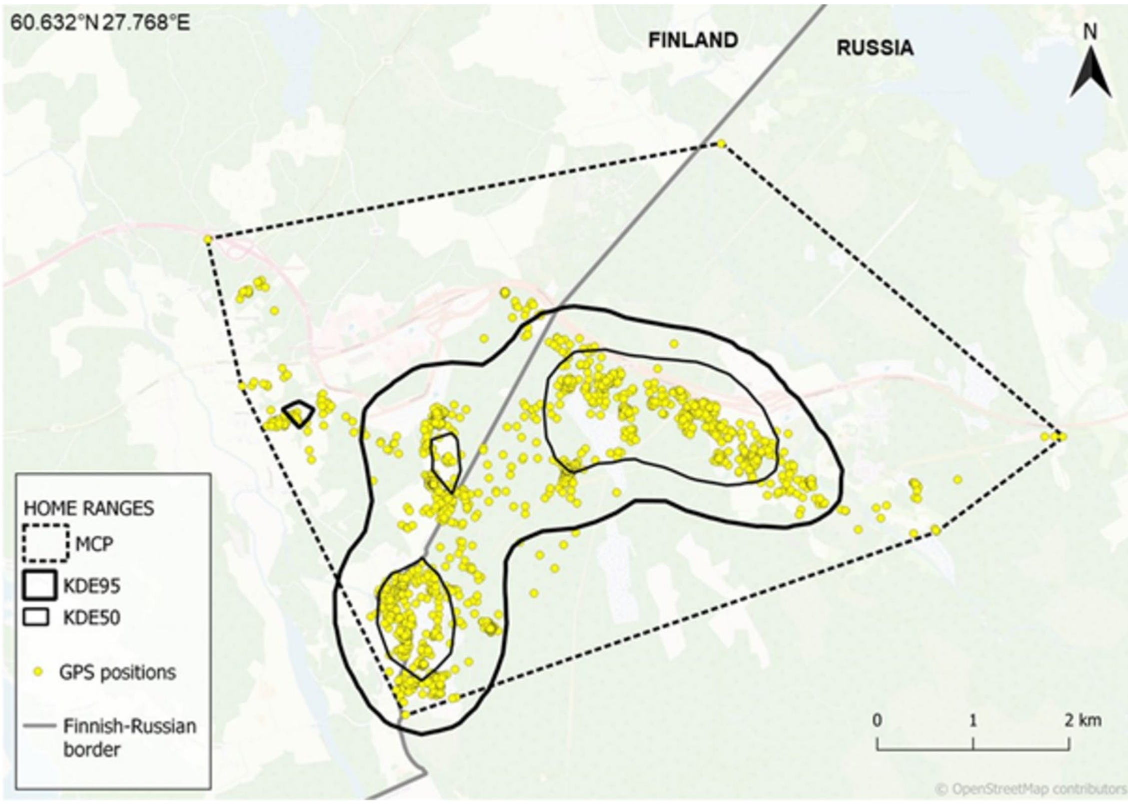

Fig. 4 Example of the home ranges of a wild boar sow (POS20) in the Finnish–Russian border zone region, near the Vaalimaa and Ylä-Urpala border stations

Home ranges and movements

As hypothesized, northern wild boars seem to roam large areas, as the home ranges in our study area were larger than those reported earlier from southern latitudes. The mean total home ranges of the studied wild boars were 1.5–8 times larger than in previous GPS-based studies from Europe (Fattebert et al. 2017; Peris et al. 2020; Gaudiano et al. 2022) and USA (Adkins and Harveson 2007; Schlichting et al. 2016; Froehly et al. 2020). The same phenomenon was also seen in the average core area sizes of both sexes. Core areas are reportedly around 1 km^2 in size for wild boar females in Italy (Gaudiano et al. 2022), while the core areas of sows in our study were around six times larger. Movement patterns of wild boars are known to vary according to season, sex, age, food availability, population density, and human pressure (such as hunting and urbanization; Massei et al. 1997; Truvé and Lemel 2003; Thurfjell et al. 2013, 2014; Bisi et al. 2018; Amendolia et al. 2019). Wild boar males have larger home ranges than females (Morini et al. 2014; Laguna et al. 2021; Clontz et al. 2022; Friesenhahn et al. 2022; Cavazza et al. 2023; this study). In addition, adult wild boars are considered to be relatively sedentary, moving short daily distances within their home ranges (Keuling et al. 2008b), which was also seen in our study. Even though the home ranges were larger, the average daily distances (5.4 km) traveled by wild boars in our study were quite typical. Average daily distances are shown to vary from 2.9 km up to 12.9 km in southern Europe, depending on habitat type (Podgórski et al. 2013; Jánoska et al. 2018). The longest direct distance moved by a wild boar from a capture site that we observed during this study was 27 km. Despite the site fidelity of wild boars, the species also has the potential for greater displacement. Major movements (tens of kilometers) are undertaken more often by dispersing juvenile males (Truvé and Lemel 2003), but occasionally extreme long-distance movements are also performed by adults. One of the longest documented movements of wild boar individuals was by a sow with piglets, which traveled some 500 km from the capture site (Jerina et al. 2014).

The larger home range sizes of wild boars in our study area compared with southern latitudes are probably related to resource availability, as presumed in our hypotheses; larger areas are needed for finding food and shelter in relatively poorer northern habitats, whereas higher-quality habitats with highly productive biotic communities are typically associated with smaller home range sizes. Therefore, southern wild boars are able to maintain small home ranges in high-quality habitats (Clontz et al. 2022). Latitude has been observed to influence home range size among other ungulates in previous studies (e.g., Anderson et al. 2005; Morellet et al. 2013), and these observations are explained by resource availability due to decreased primary productivity with increasing latitude. In addition to scarce resources, the low population density in northern latitudes may result in larger home ranges (Massei et al. 1997; Kjellander et al. 2004).

Circadian and seasonal patterns

Activity peaks of the studied wild boars occurred during or after sunset, and lowest activity took place between morning and afternoon, which confirms our hypothesis and earlier findings on wild boars' crepuscular and nocturnal activities and typical daytime resting, especially in areas with high human disturbance (Boitani et al. 1994; Lemel et al. 2003; Campbell and Long 2010; Brivio et al. 2017; Johann et al. 2020; Gaudiano et al. 2022). Wild boars are known to be more diurnal in the absence of human disturbance (Russo et al. 1997; Keuling et al. 2008a). In our study, the mean percentage of daily activity time was 50%, which fits into the 40–65% activity observed in previous wild boar studies (Massei et al. 1997; Russo et al. 1997; Johann et al. 2020). According to Laguna et al. (2021) and Cavazza et al. (2023), wild boar males are more active, but the difference between sexes was non-significant in our study, with females averaging even slightly more activity time during the summer months.

The main seasonal differences in wild boar activity in this study occurred in the length of daily activity time. In winter and spring, the studied animals reduced their activity quickly after the nightly peak, potentially to reduce their energy consumption in harsh environmental conditions and low resources. During the growth season in summer and afterwards in autumn, the activity remained at higher levels longer into the morning, which is in line with our hypothesis. Lemel et al. (2003) and Johann et al. (2020) showed that snow and temperatures have notable effects on the daily activity and movement of wild boars, while Friesenhahn et al. (2022) linked wild boar movement to crop growth stages. Access to supplemental food resources, especially during the winter, is also suggested to affect wild boar movements (Boitani et al. 1994; Oja et al. 2014; Muthoka et al. 2022). In our study, when activity times were short during the winter, the short daily travels seemed to be directed towards supplementary feeding locations.

Border zone

All the studied border region wild boars showed continuous transboundary movements, as hypothesized, with most of their home ranges (especially the core areas) being predominantly on the Russian side. Wild boars captured on the Finnish side of the border spent nearly 80% of their time in Russia. Daytime locations were mainly based within the border zone of Russia, and visits to Finland focused on the night-time. This was also seen in activity: wild boars were active during 58% of their GPS location fixes in Finland, but only moved during 43% of the fixes from the Russian side of the border. The nocturnal trips to Finland were highly associated with exploitation of available food resources such as supplementary feeding sites and crop fields. Furthermore, the two study animals in the interior part of Finland occupied larger home ranges than any individual in the border region (boars BLA21 and BLA 22, Supplement 1). This may suggest that wild boars in the interior study area are forced to occupy larger home ranges to account for the lack of refugia from hunting and other human disturbances (Keuling et al. 2008a; Thurfjell et al. 2013).

Globally, many transboundary frontiers support high levels of wildlife species and play important roles in ensuring ecological connectivity by allowing animal population movements (Liu et al. 2020). The Finnish–Russian border is also known to be an important contributor to the connectivity of many native species (Lindén et al. 2000; Aspi et al. 2009; Kopatz et al. 2014), but it additionally provides a pathway for the dispersal of novel species like the wild boar (Kukko et al. 2018). On the Finnish side of the border, forest patches are smaller and agricultural fields abundant, whereas the Russian side is characterized by continuous mature forest landscape (Muukkonen et al. 2009). In addition, the Finnish border zone is narrow, which allows higher levels of hunting pressure and human disturbance near the border, while the Russian border zone is several times wider and human activity is strictly restricted (Finlex 416/2022; Law of the Russian Federation 4730). Therefore, the Russian border zone seems to provide a refuge for wildlife, while the Finnish side appears to provide wild boar with food resources.

ASF transmission risk

Free-ranging wild boars have an important role in the spread of ASF and potentially in its persistence (Gavier-Widén et al. 2015; Iglesias et al. 2016; Taylor et al. 2020; Abrantes and Vieira-Pinto 2023), although slightly opposing findings have also been reported (Podgórski and Śmietanka 2018). Still, the border zone forms a potential pathway for ASF entering Finland via wild boars, as ASF is currently spreading in both wild and domestic suids in Russia (Cwynar et al. 2019). Pork product imports from Russia to Finland have therefore been banned (Finnish Food Authority 2022). However, wild boars also utilize anthropogenic food sources that may be contaminated with the ASF virus. For example, individual wild boars in this study sojourned at and returned frequently to truck parking areas close to border crossing points, which suggests the boars may be feeding on potentially contaminated food sources discarded by truck drivers (see Fig. 4). Collectively, the comparably large home ranges coupled with the continuous transboundary movements increase the risk of ASF spreading to Finland via wild boars. Of the human-induced food sources, both incidental (garbage) and intentional (supplementary feeding) sources may pose an ASF risk by attracting wild boars to otherwise unfavorable environmental conditions and by providing potential transmission sites.

As greater movement capacity may increase the risk of ASF spreading to new areas, the large home ranges of adult wild boars shown in this study may indicate even greater risks regarding juveniles, which typically move even further than adults (e.g., Truvé and Lemel 2003). Unfortunately, small-sized and growing wild boars cannot be equipped with collars due to animal welfare issues, and therefore alternative tracking devices would be needed to estimate ASF risks related to juvenile movements. Our preliminary results from GPS ear tags indicate the broader movements of juveniles, with direct distances up to 65 km from capture sites.

Conclusions

Overall, this study provided novel insights into the spatial behavior of wild boars, which leads to a better understanding of the spatial ecology of the species in the northernmost edge of its global distribution range and provides a baseline for future research. The movement capacity and spatial behavioral patterns of the species, coupled with the common use of human-induced food, may induce the transboundary spread of diseases such as ASF. This is further exacerbated by the larger home ranges of northern wild boars. Our results, therefore, may be used to enhance the evaluation, monitoring, and mitigation of potential disease risks. In addition, the results emphasize the importance of transboundary collaboration in the monitoring and management of wild boar populations and related risks in boreal border regions.

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Author contribution All authors contributed to the study conception, design, and data collection. Analysis and the first draft of the manuscript were prepared by Miettinen E, Melin M, and Kunnasranta M. All authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data availability The datasets generated and analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Competing interests The authors declare no competing interests.

Permits and animal welfare The capture and handling procedures of wild boars were permitted and performed following a protocol approved by the Project Authorisation Board (permit number ESAVI/4904/2020) and the Finnish Wildlife Agency (permit number 2020–7-000–25421-0). Animal welfare was supervised by a designated veterinarian and by the Animal Welfare Body of the Natural Research Institute Finland.

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