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# Intensive hunting pressure changes local distribution of wild boar

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***Abstract:*** Wild boar (*Sus scrofa*) is now an important species of wild ungulates in Central Europe. Next to conflicts of wild boar with agriculture, the main threat of wild boar presence lies in the expansion of African swine fever across Europe. The regulation of the wild boar population is complicated by the high reproduction rate and intelligent behavior of the species, which limits hunting effectiveness. We analyzed the spatial behavior of wild boar in an environment with a lack of natural food resources. The study area consisted of a forest complex (1,283 ha) with 2 areas. In the "risk" area, wild boar were intensively hunted, and in the "refuge" area, the hunting pressure was much lower. The distribution of wild boar was not regular within the study area. The wild boar density was higher in the refuge area than in the risk area. Even in times of food shortage, wild boar avoided the area where obtaining quality food was associated with a high risk of being killed. The conclusion applies to the winter season and an environment where the wild boar can become sufficiently fattened in the crop fields in the summer. For effective control of wild boar populations, it is therefore essential to organize the coordination of hunting pressure evenly in large areas.

***Key words:*** African swine fever, Europe, feeding, habitat, migration, *Sus scrofa*

In Central Europe, the wild boar (*Sus scrofa*) is an autochthonous species of game that finds ideal living conditions in the current cultural landscape and occurs in a very high density locally (Náhlik et al. 2017). Due to its high adaptability (Jansen et al. 2007), excellent reproductive potential (Servanty et al. 2007, Drimaj et al. 2020), migration potential, and ability to utilize a wide variety of foods (Herrero et al. 2006), wild boar are viewed as a species with an invasion potential in a number of places (Massei et al. 2011, Engeman et al. 2013). The growing number of wild boar also increases the importance of its conflicts with the demands of modern human society, particularly with damage to agriculture, wild boar–vehicle road accidents, biodiversity disturbance of the environment, and the risk of the spread of human and animal diseases (Gortázar et al. 2006, Herrero et al. 2006, Hladíková et al. 2008).

The wild boar is ancestral to the domestic pig. The domestic pig is an important human food, and pork production is a significant part of the national economies for many countries. Currently, the wild boar is a major disease reservoir in the spread of African swine fever (ASF) in Europe and is also a primary threat to the transmission of ASF to domestic farms (e.g., Costard et al. 2015), which has serious implications for agricultural and food production. It is very difficult or even impossible to eliminate an infected local population of wild boar (Garcia-Jimenez et al. 2013). When ASF is transferred to the wild boar population, it is always necessary to assume that, even in ideal conditions, it will take months or years to eliminate the disease. In addition, due to hunting disturbance, there is a high risk of expanding the infected area (Gogin et al. 2013, Nurmoja et al. 2017). One of the most important factors is the density of wild boar populations, which affects both risks of transmission of ASF and the success of eradication (More et al. 2018). In the event of infection, large populations pose higher risks of spreading the disease to other areas, which leads to higher mortality, subsequent liquidation of more animals, and prolonging the eradication period. Before commencing control measures, it is necessary to determine precisely the desired rate of reduction of the individual population.

The spatial activity of the wild boar depends mainly on the food supply (Oja et al. 2014). During the vegetation season, the wild boar moves to field crops, where it often stays until autumn and has a calm life, protected by summer cover, making the hunting of wild boar difficult or impossible (Keuling et al. 2010). In winter, it returns to the forest, where its predominant foods consist of forest mast (acorns [*Quercus* spp.] and beeches [*Fagus sylvatica*]; Schley and Roper 2003). In food-poor areas, the wild boar suffers under-nutrition, and over-winter survival requires use of the fat stores accumulated during the summer (Vetter et al. 2015, Brogi et al. 2021). In most areas of Central Europe, wild boar are managed by hunting, and in the winter wild boar are offered supplementary feed (Keuling et al. 2008*a*, Oja et al. 2014, Ježek et al. 2016, Mikulka et al. 2018). Throughout the winter, wild boar then stay close to the feeding locations, which provide most of the necessary food (Geisser and Reyer 2005, Plhal et al. 2014*b*, Drimaj et al. 2019). The association with feeding sites and limited spatial activity in winter is probably related to the tendency of animals to prefer saving energy than wasting it looking for unreliable food sources (Hofmann 1989, Massei et al. 1997, Lemel et al. 2003). Looking for scattered food sources in winter is connected not only with considerable energy losses but also puts an individual at a higher risk of being hunted (e.g., Thurfjell et al. 2013). For this reason, the wild boar, in this period, reduces its home range by half and migrates for food only for very short distances (Massei et al. 1997).

The wild boar distribution is also significantly influenced by human disturbances and especially the intensity of hunting (Thurfjell et al. 2013). Wild boar adapt to given sources of disturbances by switching to a strictly nocturnal way of life or migrating for food over considerable distances (Sodeikat and Pohlmeyer 2003, 2007; Focardi et al. 2020; Johann et al. 2020). The only widely applicable tool for the regulation of wild boar populations has traditionally been lethal control by shooting (Keuling et al. 2013), which must be applied in a possible optimum intensity (Servanty et al. 2009). However, the effectiveness of hunting depends on a number of factors (Keuling et al. 2008*b*), and experience to date shows that there is no significant reduction in the number of wild boar (Massei et al. 2015). The wild boar is a highly intelligent animal that can adapt its behavior to minimize the risk of hunting (Thurfjell et al. 2013). It always considers optimizing food intake and tolerable risk of being killed by hunting.

The aim of the presented study was to analyze the behavior of the wild boar in an environment that is poor in natural food sources. In the entire area, the wild boar was supplementary fed. In part of the area, the wild boar was intensively hunted, causing disturbance, and the other part of the area had calm, non-intensive hunting. We tested 2 hypotheses: (1) the density of wild boar will be the same in both parts of the area, because there is the same food supply and (2) the density of wild boar will be higher in the part of the area where hunting is only sporadic than in the part of the area where the wild boar is intensively hunted. The results will help to clarify some features of wild boar behavior that can be used to increase the efficiency of its hunting.

## Study area

The study was conducted on an area of 12.83 km$^2$ in a forest complex in the southern part of the Czech Republic (-49°15'52.643"N, 15°37'46.266"E; Figure 1). The area was part of a total study area of 39 km$^2$ (including agricultural areas). This forest complex is surrounded by fields and is situated at an altitude of 550–650 m. The forest stands are highly homogenous: 92% Norway spruce (*Picea abies*), 5% beech, 3% pine (*Pinus sylvestris*), 2.2% alder (*Alnus glutinosa*), and others <1%. Natural tree regeneration prevails as the preferred regeneration method. Owing to the dominant spruce management, the shrub and herb layers are very poor, and in places virtually non-existent. Large carnivores

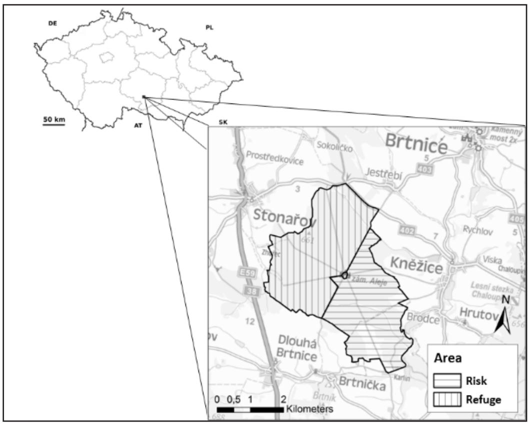


**Figure 1.** Location of the study area in the southern part of the Czech Republic, sub-divided into risk and refuge areas.

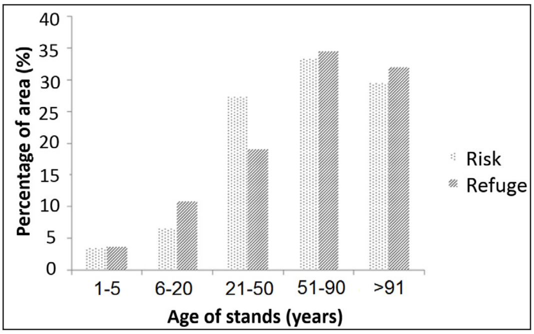


**Figure 2.** The proportion of individual stand age categories on transect in the study area, Czech Republic.

do not occur in the area. Wild boar migration outside the study area takes place only during the vegetative season, when wild boar move to the surrounding fields, moving back to forests after the harvest. Outside the vegetation season, food sources in the forest are considerably limited and artificial feeding at feeding sites, typically with maize (*Zea mays*), can be considered the only significant quality food source.

The area was divided into 2 parts with different management of wild boar (Figure 1). The refuge area covers 739 ha, and the risk area covers 544 ha. The forest stand structure in both areas was similar. Artificial feeding sites are distributed evenly throughout the study area, and feeding intensity at individual sites was the same. Two years ago, the winter density in the study area (i.e., forest area) was estimated at 64.3 individuals per km$^2$ (Plhal et al. 2014*b*). The area available to these wild boars was 39 km$^2$ (study area including the surrounding agricultural areas). The age composition of forest stands was similar in both areas (2-sample Kolmogorov-Smirnov test; $P = 0.1448$ and $P = 0.4838$, respectively; Figure 2).

## Methods

The hunting management in both areas was assessed by local managers recording all hunting and feeding-related activities throughout the main hunting season. The assessed characteristics included: intensity of hunting (individual/collective hunts), number of feeding sites, type, and quantity and quality of food along with frequency of feeding. Hunting intensity was recorded in the form of hours spent on individual hunts (mostly still hunting at baiting sites) and also the number of collective hunts. Collective hunts in both areas were similar in terms of number of hunters and the use of hunting dogs (*Canis lupus familiaris*). Natural food quality and quantity in both areas were the same. Hunting intensity was significantly higher in the risk area than in the refuge area (Table 1).

### Wild boar distribution

Wild boar distribution during the winter was evaluated according to the occurrence of their fecal pellet groups (FPG) in spring. The length of the fecal accumulation period was determined by the presence of the wild boar in the monitored forest complex on a stable basis (monitoring was conducted at weekly intervals) and the end of the decomposition period (Drimaj 2014).

Prior to field monitoring, a base map for Global Positioning System (GPS) receivers was created in ESRI ArcGIS 10.1. This map contained boundaries of the study area and included a system of north-south lines 100 m apart. The total length of transect within the forest stands was 119 km. This design of data collection eliminates the individual impact of counters on the choice of monitored plots. The base map with transect was uploaded to GPS units (Trimble Juno ST equipped with TerraSync Pro field software), which were then used for field navigation. The FPG were counted within the study area on April 2–3, 2014, a week after the disappearance of snow cover. Every counter (a total of 5 people) was provided with a GPS unit with a base map and transect and was proportionally assigned part of the transect for monitoring

**Table 1.** Hunting management in the risk and refuge areas, Czech Republic.

| Area | Intensity of hunting in winter season | | Number of feeding sites | Quality of food | Quantity of food (kg per feeding site per month) | Intensity of feeding (events per month) |
|---|---|---|---|---|---|---|
| | Individual (hours per month) | Collective (events per month) | | | | |
| Risk | 360 | 6 | 10 | High[a] | 250 | 20 |
| Refuge | 30 | 1 | 10 | High[a] | 250 | 20 |

[a] Corn (*Zea mays*) grains, beets (*Beta vulgaris*), and wheat (*Triticum aestivum*) were supplied in both areas.

FPG within 2 days in a 2-m strip. Each FPG was spatially localized using GPS and recorded in an attribute table in the digital geo-database (in cases when FPG density was higher at a given place, the exact number of pellet groups was recorded with reference to the given point). During the field monitoring, the positions of all feeding sites within both areas were also recorded.

## Data analysis

We used ArcGIS 10.1 for spatial analysis of forest stands and to produce a map. For the statistical analysis, we divided the transect into regular rectangular plots of 2 × 20 m. These plots were then intersected by the polygon areas (risk and refuge) and age categories of the forest stands using the intersect tool. The area of each resulting component plot was calculated using the calculate geometry tool (if the component plot was intersected by an area or age class boundary, only the real area of the theoretical 40 m$^2$ was included). We summarized the number of pellet groups within each plot using the spatial join tool. In the next step, the original polygon layer was converted into centroids, which contained all the attribute data of individual component plots (area identification, age category, number of pellet groups and plot). Finally, these centroids were subjected to spatial analysis using the point distance tool, which calculated their distance to the nearest feeding site.

One of the final outputs of the GIS analyses described above was a table, which accompanied each centroid with relevant attribute data on the area, age, number of pellet groups, and the distance to the nearest feeding ground. This tabular data was subject to further statistical processing and evaluation.

The wild boar population density was calculated according to the following formula (Plhal et al. 2014*b*):

$$PDi = \frac{x_i}{AP \times DDR} \times P_i$$

where $PD_i$ = population density for study area; $x_i$ = average FPG density per hectare (FPG per ha); $AP$ = accumulation period (145 days); $DDR$ = daily defecation rate (5 FPG per day per animal; by Plhal et al. 2014*a*); and $P_i$ = study area (ha).

Based on their age (shelter potential for wild boar, respectively; Fonseca 2008, Plhal et al. 2014*b*, Drimaj et al. 2019), the forest stands in the study area were divided into 5 groups: very young forest stands / young plantations (1–5 years old, low saplings, inconvenient for wild boar due to very limited cover), young forest stands / older plantations (6–20 years old, high and dense stands with optimum cover conditions), middle-aged forest stands (21–50 years old, high and open stands), ripening forest stands (51–90 years old, unsuitable for wild boar save for the presence of natural regeneration), and mature forest stands (≥91 years old, open stands with undergrowth, potential food sources and natural regeneration).

Counters checked 136.9 km of transects (27.4 ha; 2.14% of the study area). The total time consumption of 5 counters was 100 hours. The length and area of transect had to be further reduced to eliminate non-forest land (roads, water bodies, fenced plots, etc.), which reduced the total stand area to 24 ha.

## Statistical data processing

The representation of individual stand age classes within both areas and within individual transect was compared using the 2-sample

**Table 2.** Estimated parameters and goodness of fit criteria of final generalized linear models with negative binomial distribution for the number of pellet groups in the risk and refuge areas, Czech Republic. $a$ – estimated intercept of the model; $b$ – estimated model parameter for explanatory variable distance from feeding site; $v_{ij}$ – estimated model parameter for explanatory variable stand age >20 years; AIC – Akaike information criterion.

| Area | Parameter | Estimation | $P$ | Pseudo $R^2$ | AIC |
|---|---|---|---|---|---|
| Risk | $a$ | -0.0089 | 0.0048 | 14.3 | 2,652.8 |
| | $b$ | -0.0028 | <0.0001 | | |
| Refuge | $a$ | 1.5040 | <0.0001 | 13.6 | 6,186.1 |
| | $b$ | -0.0021 | <0.0001 | | |
| | $v_{ij}$ | -1.5002 | <0.0001 | | |

Kolmogorov-Smirnov test. The dependence between the number of pellet groups, distance from feeding grounds, and stand group age were evaluated by generalized linear model (GLM) with the negative binomial (NB) distribution (Zuur et al. 2009). Stand age was used in the model in the following way: the first group (youngest stands) was used as the reference group (e.g., intercept), and other groups were compared to it. The models were created separately for individual areas. The GLM with NB distribution follows Zuur et al. (2009):

$$E(Y_{ij}) = u_{ij}$$

$$u_{ij} = e^{(a+b*X_{ij}+v_{ij})}$$

where $E(Y_{ij})$ = mean value of the distribution of the number of pellet groups on plot $i$ in area $j$; $u_{ij}$ = fitted mean for the negative binomial count data; $a$, $b$ = estimated parameters of the model; $X_{ij}$ = distance of plot $i$ from a feeding ground in area $j$; and $v_{ij}$ = parameter estimate for the age of stand group that houses plot $i$ in area $j$.

The impact of distance from the feeding site on pellet group density in the studied stand group age was tested by the multiple comparison method. All results were tested at significance level $\alpha = 0.01$.

## Results

A total of 1,851 records were made on this area (outside feeding sites), representing 3,434 wild boar FPG. The total FPG density on the studied area was 143 FPG/ha.

In the risk area, stand age did not affect number of pellet groups ($P > 0.01$ in all age categories). The final model of number of pellet groups for the risk area was influenced therefore only by distance from feeding site, used as an explanatory variable. In the risk area the number of pellet groups decreased with increasing distance from feeding sites regardless of the stand group age. Estimated parameters and goodness of fit criteria of final model are reported (Table 2).

In the refuge area the FPG number was influenced both by distance from the feeding site and by stand age. However, using a multiple comparison test of the resulting fitted values obtained for 5 different categories of age groups revealed no difference between the resulting fitted number of FPG in age groups 1 and 2 ($P$ = 0.6710) and age groups 3, 4, and 5 to each other ($P < 0.01$ for all values of pairwise comparison). Therefore, all stands can be divided into only 2 groups based on their age: up to 20 years and >20 years. The number of FPG in these 2 age groups was different ($P < 0.0001$). The final model in the refuge area therefore contained the impact of distance from feeding site and stand age, represented by 2 groups divided into ages up to 20 years and >20 years (*vij*), respectively. Estimated parameters and goodness of fit criteria of final model are reported (Table 1). The resulting fitted values and their confidence intervals are also shown (Figure 3). From achieved results (Table 2; Figure 3), it is evident that in the refuge area the number of pellet groups decreases with increasing distance from the feeding site and with increasing age of the given stand group.

Based on the likelihood ratio test comparing the goodness of fit criteria of the final models ($P < 0.0001$), we can say that the number of FPG in

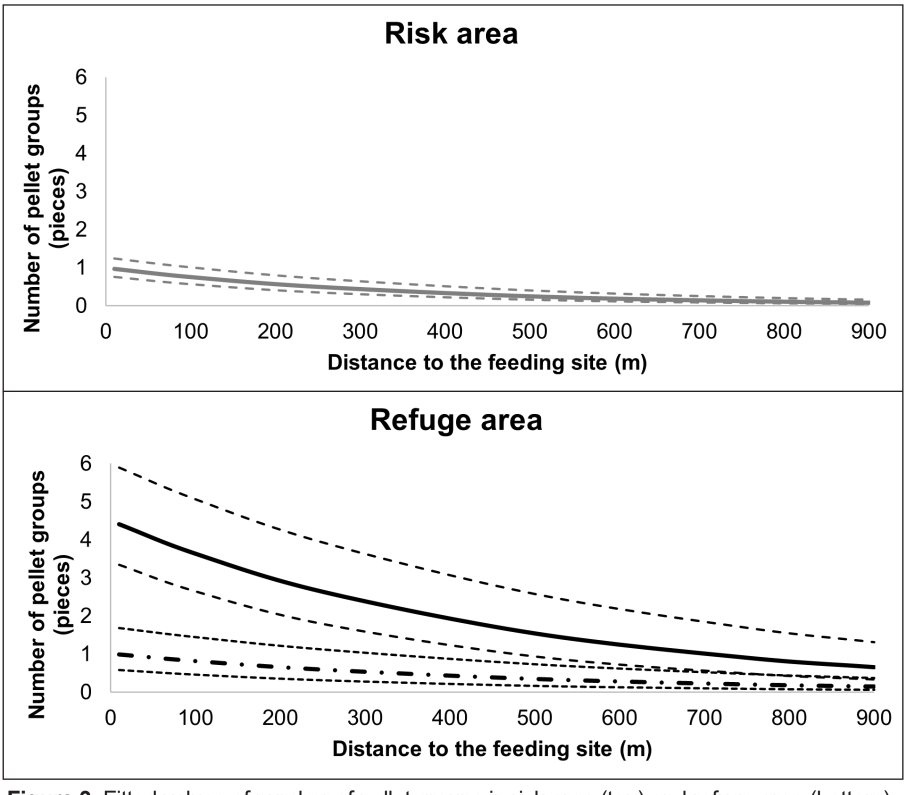


**Figure 3.** Fitted values of number of pellet groups in risk area (top) and refuge area (bottom). Grey solid line – fitted values for the number of pellet groups in forest stands; grey dashed lines – confidence intervals of these values; black solid line – fitted values for the number of pellet groups in forest stands of up to 20 years; black dashed lines – confidence intervals of these values; black dot-and-dash line – fitted values for the number of pellet groups in forest stands older than 20 years; black dotted lines – confidence intervals of these values.

the risk area is not the same as in the refuge area.

The wild boar winter population in the whole study area was estimated at 238 individuals (i.e., 18.6 per km$^2$), with 176 individuals in the refuge area (23.8 per km$^2$), and 62 individuals (11.4 per km$^2$) in the risk area.

## Discussion

Wild boar distribution was assessed using the method of one-off pellet group count at the end of the winter season. This method is commonly used in estimating the abundance of large ruminants; it has a number of advantages, but it also requires a number of conditions that must be fulfilled to get sufficiently accurate data (Neff 1968, Mayle et al. 1999, Engeman et al. 2013). In our case, the most important conditions to ensure the obtaining of objective results were met. The count was conducted on an area representing 2% of the study area, the transect covered the study area, and the stand structure on the monitored plot did not differ from stand structure on the total area. In this study, wild boar concentrated in the vicinity of supplementary feeding sites, as no substantial natural food sources were available in the predominantly coniferous stands. Similarly, wild boar in mixed upland forests were dependent on supplementary feeding sites in periods of snow cover, regardless of the fact that the area encompassed old beech stands with a supply of beechnuts (Plhal et al. 2011). Wild boar in the study depended purely on food sources at supplementary feeding sites, which made their association with these places relatively close in both areas. It was assumed that wild boar did not migrate outside the forest complex (Plhal et al. 2014*b*) in search of food, despite the fact that in some types of environments and under certain conditions wild boar may migrate for long distances (Singer et al. 1981, Boitani et al. 1994, Podgórski et al. 2013). It was therefore assumed that FPG density would be higher in young stands, which offer better cover, than in old stands. Moreover, supplementary feeding sites were usually established in the vicinity of stands providing cover, and the wild boar did not have to migrate far. In accordance with this assumption, wild boar FPG density was higher in young stands than in old stands. However, the difference in the risk area was not statistically significant. In this part of the study area, which was subject to higher hunting pressure, the smaller difference in FPG density between particular habitats was probably due to less intensive use of cover within the stands. In general, cover-providing stands were less used in the risk area than in the refuge area with lower hunting pressure.

Our results confirmed that wild boar are highly sensitive to hunting pressure and are capable of adjusting their movements and spatial behavior under such threat, as similarly stated in Keuling et al. (2008*b*). Food and cover are the 2 fundamental factors influencing wild boar distribution in an environment where the animals are subject to hunting pressure (Boitani et al. 1994, Tolon et al. 2009, Podgórski et al. 2013). The wild boar in our study area were able to distinguish both parts of the study area, which were identical in composition of vegetation and were divided by only 1 of many inconspicuous forest paths. Both food availability and cover were similar in the risk and refuge areas, aside from the fact that the quality and quantity of food do not necessarily play a major role in times of need. Intense hunting pressure in 1 part of the forest complex (risk area) led to a large proportion of the wild boar moving to a quiet part (refuge area), where they were more than twice as numerous, which resulted in competition for food. While in the risk area the supplementary food on the baits remained unused, in the refuge area the wild boar had significantly less food available, due to greater competition for food sources. Wild boar behave similarly in other areas where intensive hunting take place and wild boar become predominantly nocturnal, remain hidden during the day, and change spatial distribution (Spitz and Janeau 1990, Keuling et al. 2008*b*, Podgórski et al. 2013, Thurfjell et al. 2013). Because the collective hunts were used in the whole study area, wild boar did not respond by changing resting places (Tolon et al. 2009). Intensively used tracks in snow between both risk and refuge areas were detected within the total study area. This finding verifies the different pellet group distribution in the study area. The major part of the wild boar population then only (daily) migrated in search of food at supplementary feeding sites in the risk area but then immediately returned to the refuge area for resting throughout daylight. This is corroborated by the fact that within the risk area the highest FPG density could be found along the boundaries with the refuge area.

## Conclusion

We confirmed that the wild boar sensitively reacts to hunting pressure. The density of wild boar was lower in intensively managed areas and higher in low-risk areas. Uneven intensity of hunting leads to uneven distribution of wild boar. In conditions of winter hardship with a lack of food resources, the wild boar preferred starvation to obtaining hearty food, which was associated with a high risk of hunting. Due to the successful reduction of wild boar populations, it is therefore essential that hunting pressure should be even throughout the area inhabited by the local population.

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