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Research Article

Muddy business: seasonal use of wallows by wild boar recorded by camera traps

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Abstract

Mud wallowing is an important comfort behaviour for wild boar (Sus scrofa), having several functions. Yet, the temporal changes of when wild boar visit mud wallows and how they use these areas has been rarely studied. To investigate seasonal and daily activity patterns and behaviour of wild boar at mud wallows, passive monitoring involved camera traps set up at ten natural wallows and eight rubbing trees in central Croatia over the course of a year, and the findings were compared with 40 random locations. The most animals were recorded at the wallows in spring and the fewest in winter. The relative abundance index at the wallows was highest in spring but showed no significant seasonal difference. Wild boar significantly preferred coniferous to deciduous trees for rubbing. Behavioural analysis revealed that rooting was most frequent at the wallows in spring, wallowing behaviour dominated in summer and autumn, and locomotion was predominant in winter. Activity patterns showed predominantly nocturnal activity at all sites, with a peak of activity around sunset, except for the wallow during summer when activity was mostly diurnal but peaking around sunset. Overall, there was a high overlap in activity patterns between the wallows and random sites, with the lowest overlap in summer due to increased diurnal use of wallows. A similar overlap was observed in autumn and winter. These findings highlight the multifunctional role of wallows and rubbing trees in wild boar behaviour, suggesting that targeted monitoring can serve as an effective tool for ecological research and population management, including applications in disease surveillance and control.

Introduction

Wild boar (*Sus scrofa*) is described as intelligent and secretive animal that exhibits a variety of behavioural patterns (Morelle et al., 2015). The most common behaviours of wild boar include foraging activities (such as rooting and feeding) accompanied by locomotion (Erdtmann and Keuling, 2020). Comfort behaviours, such as wallowing, are generally less practised but are considered crucial for wild boar well-being (Keuling and Stier, 2009; Bracke, 2011). Wallowing is defined as the covering of the body surface with mud or a mud-like substance and it serves several functions, including the removal of ectoparasites by immersion in mud and subsequent rubbing, thermoregulation, sexual function, scent marking, and wound disinfection (Krže, 1988; Fernández-Llario, 2005; Bracke, 2011; Gray et al., 2019; Ruf et al., 2023). Tree-rubbing is another behaviour closely related to wallowing, and it shares a common function for removing dried mud, hair, and ectoparasites, and for intraspecific communication by leaving scent marks (Bracke, 2011; Ichen et al., 2024). The link between these two comfort behaviours is also evident from the presence of rub/scrub trees in close proximity to wallows (Mayer, 2009). However, little is known about the factors influencing the selection of trees for rubbing by wild boar (Lee and Lee, 2014), they most often use conifers, as the combination of coniferous resin and mud may create a protective layer on the body in case of injury (Krže, 1988).

Wallows are small oval or elongated depressions in moist soil (mud pits) or in small streams with a shallow water level (Belden and Pelton, 1976; Massei and Bowyer, 1999; Mayer, 2009). They are primarily created by animals rooting, rolling, scratching and displacing the soil, creating an impermeable layer of soil that retains water over a longer period of time. Wild boar typically use the same wallow throughout the year, and even twice daily in the warmer months (Campbell and Long, 2009; Bracke, 2011). The use of frozen wallows has also been observed, as wild boar break up the ice (Stegeman, 1938). The importance of the wallows is further seen by the fact that wild boar often leave the area when they dry out (Hörning et al., 1999). Wallows are used by different age and sex groups of wild boar, but mostly by adult males during the mating season (Fernández-Llario, 2005). The frequent use by large numbers of wild boar may represents a potential reservoir for pathogens in both wallows and the surrounding streams (Belden and Pelton, 1976). This is particularly important in outbreaks of African swine fever, where it has been reported that the virus causing this disease can sustain virulence in water and soil for an extended period of time, making wallows a potential site for the spread of infection (Varzandi et al., 2024).

The most common wild boar ectoparasites, especially in warm climates, are ticks and lice, and wallowing helps to form a protective layer of mud against them (Fernández-Llario, 2005). Wild boar populations can be quite heavily infested with ectoparasites, such as in Spain where 57 % of individuals were reported to be affected, and the combination of wallowing and rubbing can successfully remove a considerable number of these ectoparasites (Castillo-Contreras et al., 2022). In addition, wallowing serves to cool the body and prevent hyperthermia, especially in larger individuals (Ruf et al., 2023). Heat exchange is minimised by the limited thermoregulatory function of wild boar sweat glands in response to elevated ambient temperatures (Ingram, 1967), the presence of subcutaneous adipose tissue that provides high thermal insulation (Zervanos and Hadley, 1973), and the barrel-shaped body morphology that reduces the surface area to body mass ratio, thereby

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reducing conductive and radiative heat transfer (Bracke, 2011). Several studies have also pointed to the sexual function of wallowing, both in males (Fernández-Llario, 2005) and females (Sambraus, 1981), although it is most pronounced in males at the peak of the rut (Bracke, 2011). It has been also reported that wallowing is more frequent in domestic pigs and warthogs (*Phacochoerus africanus)* during the mating season and that males of these species have skin glands responsible for the production of pheromones that are important for mating (Estes et al., 1982). Following this idea, Fernández-Llario (2005) conducted a short-term study from October to February and concluded that the highest frequency of wallowing in wild boar coincided with the mating season, suggesting a sexual function of wallowing. However, his conclusion should be interpreted with caution as it did not cover the whole year and was based only on the visual inspection of animals after culling. The function of scent marking by urinating and lathering saliva on the substrate and nearby vegetation for territory marking and interspecies communication is also confirmed, especially during the peak of the rut (Bracke, 2011). Some authors have also suggested the possibility that wallowing could be related to wound disinfection of injuries caused by canines during mating season fights in boars (Sambraus, 1981). Though some authors have stated that wallowing can help to cover wounds and accelerate healing due to the bactericidal properties of mud (e.g., Fernández-Llario 2005), this theory has not yet been confirmed.

Knowing and understanding the seasonal activity of wild boar at wallows is of great importance for management and epidemiological control (Mayer, 2009; Varzandi et al., 2024). The aim of this study was to: *i*) analyse the relative abundance index (RAI) of wild boar at wallows and rubbing trees in different seasons, and compare them to the RAI obtained from random locations; *ii*) analyse behaviour patterns of wild boar at wallows in different seasons; *iii*) compare activity levels at wallows in different seasons. Finally, comparing activity levels and behavioural patterns of wild boar at the wallows with activity levels and patterns at random locations in the same study area will ultimately give better insight into the importance of wallowing for the biology of this species.

Materials and methods

Study area

The study was conducted in Sisak-Moslavina County in central Croatia, south of the town of Glina. The study area extends in a north-south direction over an area of about 7800 ha (between 45°8′ and 45°17′ N and 16°1′ and 16°9′ E), including the far western slopes and parts of Mt. Zrinska Gora. To the southwest, the study area borders directly Bosnia and Herzegovina. The study area is located in the belt of acidophilic beech forests (*Fagus sylvatica*) at higher elevations, while lower parts are dominated by a belt of climate zonal forests of common hornbeam (*Carpinus betulus*). The Köppen classification of this area is a "Cfwbx" climate, meaning warm and rainy with frost and snow in the winter (Zaninović et al., 2008). The average annual air temperature in the study area was 10.7 °C, with a seasonal breakdown is 15.2 °C in spring, 18.3 °C in summer, 6.1 °C in autumn and 2.7 °C in winter. The annual rainfall is around 1079 mm. The study area is interspersed with numerous creeks (13 permanent headwaters) that provide a steady supply of water for wildlife year round.

The study area is habitat for many large and small mammal species, and wild boar is the most abundant. Wild boar population density estimated using camera traps and the random encounter model was 15.3±2.19 individuals/km^2, or about 1200 individuals in the area (ENETWILD-Consortium et al., 2024). The next most common species are roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*), and fallow deer (*Dama dama*). Other large mammal species present though in lower numbers are grey wolf (*Canis lupus*), while the brown bear (*Ursus arctos*) is present only sporadically. Mesocarnivores, such as golden jackal (*Canis aureus*), red fox (*Vulpes vulpes*), and wildcat (*Felis silvestris*) are also present in the area. Wild boar are hunted individually all year round, with the exception of heavily pregnant and lactating females. Driven hunts with dogs are performed between November and February.

Data collection

Wallows were considered hollows in the ground containing mud and sometimes water year round. Ten wallows were selected, and measurements were taken with construction tape measure to the nearest centimetre; while length, width, depth and altitude were measured in metres using a GPS device (Garmin Montana 700i). Observations were performed with ten camera traps installed at the selected wallows, and eight camera traps installed at active rubbing trees near the wallows between 17 March 2023 and 25 March 2024. Once first year results were obtained, the survey at the wallows was repeated during summer (21 June to 23 September 2024) to obtain activity level and activity pattern during summer 2024. For rubbing trees, both coniferous trees [spruce (*Picea abies*) and black pine (*Pinus nigra*)] and deciduous trees [apple tree (*Malus domestica*), alder (*Alnus glutinosa*), beech (*Fagus sylvatica*), and hornbeam (*Carpinus betulus*)] were selected (Tab. S1).

Camera traps were positioned on trees about 50 cm above the ground, facing the wallows or rubbing trees. They were active 24 h a day in burst mode (three photos) without a delay between bursts. Additionally, 40 camera traps were set up in a systematic random grid to compare differences in detection between wallows and random locations that could be used as a reference point for detecting differences between comfort behaviours and other behaviours. Random locations were determined at the intersection of four cells of a grid created in ArcGIS Pro (Esri, 2024). Each cell was 2×2 km. Camera traps at these random locations were active between 15 July 2023 and 25 March 2024 to record wild boar activity levels and patterns obtained from a random study design. They were also active 24 h a day in photo mode without delay and were positioned on trees at a height between 50–100 cm, facing north to avoid exposure to sunlight. Based on the ENETWILD-consortium et al. (2023) recommendations, no visual, auditory or olfactory attractants were used to avoid affecting the presence and frequency of recording wild boar. Also, camera traps were not placed near animal and human trails. Randomly positioned camera traps proportionally covered all types of habitats present in the study site. The cameras were inspected, checked, and maintained every three months to replace batteries and memory cards.

At the wallows and rubbing trees, Browning Command Ops Pro camera traps were used with a resolution of 22 megapixels, a sensor range of 21.3 meters and a shooting angle of 55°. In the random design, Dörr Snapshot Mini camera traps were used with a resolution of 16 megapixels, a detection angle of 55º and a shooting angle of 40º. The locations of the cameras in the study area are presented in Fig. 1. Both camera trap models were equipped with an infrared flash, enabling night photos with minimal disturbance to animals. This feature allows continuous recording of animals 24 hours a day. Each camera trap recorded data such as date, time, air temperature, moon phase, and location ID. Obstacles blocking the detection area such as branches were removed to ensure clear photos.

Weather conditions and air temperature (°C) were obtained from the Croatian Hydrological and Meteorological Service.

Data analysis

Separate analyses were performed for each camera trap setup (target/random sites) and by season (spring: 21 March–20 June; summer: 21 June–22 September; autumn: 23 September–20 December; winter: 21 December–20 March). Data acquisition from photos taken at the wallows or rubbing trees was performed manually, and each observed group or individual was considered an independent record if there were more than 2 minutes between two consecutive photos. Time interval was chosen based on previous studies and guidelines (Hofmeester et al., 2017; ENETWILD-consortium et al., 2024). During the examination of photos for each independent record, data were recorded in a Microsoft Excel spreadsheet (Microsoft Corporation, 2018). The collected data included the camera trap ID, animal species, the number of wild boar in the group, date and time, and observed animal behaviour

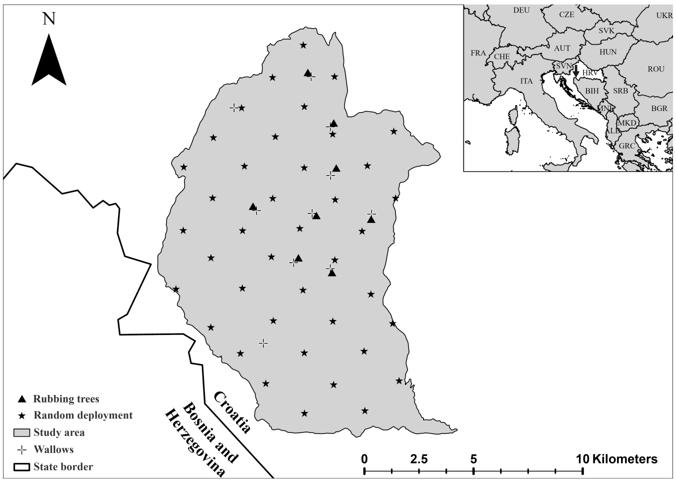

Figure 1 – Locations of the camera traps (ten wallows; eight rubbing trees; 40 random locations) in the study area (7800 ha) in central Croatia.

(wallowing, rooting, locomotion, rubbing or other). Each observed behaviour was scored, while in cases where wild boar exhibited multiple behaviour types, all were scored equally. The ethogram of wild boar behaviours in this study is shown in Tab. 1. Photos from the random camera trap locations were uploaded onto the web app Agouti where photographs were automatically grouped in sequences if there was no delay longer than 2 minutes between two consecutive photos (Casaer et al., 2019). Photos were then tagged with species and number of animals, and the camtrapdp file containing information on species, location and timestamp was generated (Hofmeester et al., 2022).

Table 1 – Ethogram of wild boar behaviour in this study.

Behaviour	Description
Wallowing	The wild boar enters a wallow and engages in body contact with the mud or water, typically by lying down or rolling in it to coat the body.
Locomotion	The wild boar moves through the camera frame without or with short pauses, without interaction with the wallow. The behaviour was classified as locomotion regardless of wild boar speed in the sequence.
Rooting	The wild boar uses its snout to dig up the soil. Rooting is characterised by repeated head movements and displacement of ground material.
Tree rubbing	Behaviour in which a wild boar rubs its body against the trunk of a tree. It was usually performed with vigorous, repeated body movements that left visible marks on the tree.
Other	Other types of behaviour exhibited by the wild boar such as lying down or interacting with other individuals.

All data analyses and result visualisations were performed in R software (R Core Team, 2023). For both camera trap setups, camera trapping days were calculated by season, and the RAI was calculated as the number of events per 100 camera trap days for each site and season, using the following formula described by O'Brien et al. (2003) and O'Brien (2011):

$$\mathrm{RAI} = \left(\frac{\text{Number of independent events}}{\text{Number of trap days}}\right) \times 100.$$

Seasonal differences in RAI across wallow, rubbing tree, and random camera trap locations were analysed using a linear mixed-effects model (LMM). RAI values were log-transformed to improve normality and homoscedasticity of residuals. The model included season (spring, summer, autumn, winter), location (wallow, rubbing tree or random), and their interaction (season × location) as fixed effects, and camera trap ID as a random intercept to account for repeated measures at the same camera locations across seasons. The model was fitted using the lmer() function from the lme4 package (Bates et al., 2015). Model assumptions were checked using standard residual plots and the DHARMa package (Hartig, 2024), confirming appropriate residual distribution and homogeneity of variances after log-transformation. Post-hoc pairwise comparisons between seasons and site types were performed using estimated marginal means (emmeans package in RStudio) with Tukey adjustments for multiple comparisons. Differences of using coniferous or broadleaf trees for rubbing events were tested using Wilcoxon rank-sum tests.

Wild boar activity level (proportion of the day the animal is active ranging from 0 to 1, i.e., 0.5 value represents that animal was active for 12 h a day) was estimated from captured photos using the "activity" package (Rowcliffe, 2023), fitting the von Mises kernel as the circular normal distribution. To account for the circularity of time, the solar time at which each photo was taken was converted to radians, ranging from 0 to 2π, representing a circular, random variable. Based on the simulation performed by Ridout and Linkie (2009), several smoothing parameters (0.5 to 2) were plotted against the original data points. Based on visual inspection, a smoothing factor value of 1.5 was selected. Standard error was estimated by non-parametric bootstrapping (999 bootstrap iterations). An activity probability distribution was then created from fitted activity models to illustrate the activity pattern. To statistically compare activity levels across seasons and setups, the Wald test was used to evaluate whether the difference between two activity estimates (a_1 and a_2) was significantly different from zero. The test statistic was calculated as $W = (a_1 - a_2)^2/(SE_1^2 + SE_2^2)$, where SE_1 and SE_2 were the standard errors of the respective estimates. This statistic follows a chi-squared distribution with 1 degree of freedom. To check for differences in activity patterns between wallows and random datasets, the overlap coefficients of temporal activity patterns were estimated according to Ridout and Linkie (2009) with the function "overlapEst" from the package "overlap" (Meredith et al., 2024).

Results

The average size of the wallows in this study was 273×201 cm, with a depth of 22 cm, at an average elevation of 319 metres (Tab. S2). The highest number of animals at wallows was recorded in spring ($N = 679$; 235 independent events) and the lowest in winter ($N = 369$; 188 independent events) (Fig. 2). The RAI at the wallows was highest in spring, with camera traps recording an average of 53.76 ± 12.95 events per 100 days. The lowest RAI at the wallows occurred in winter, with cameras recording an average of 33.63 ± 13.72 events per 100 days. The RAI did not differ significantly ($p > 0.05$) across seasons for the wallows data set (Fig. 2). At random locations, RAI was highest in summer (52.99 ± 6.67 events per 100 days and lowest during autumn (22.88 ± 3.73). There were no significant ($p > 0.05$) seasonal differences in RAI between sites. RAI at random locations was significantly higher during the summer ($p < 0.05$) in comparison with other seasons. Visual representation of calculated RAI during all seasons and locations is shown in Fig. 2. Detailed results of the model are available in Tab. S3 and S4.

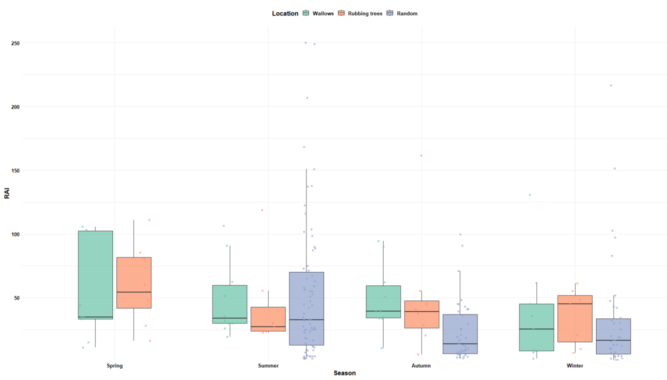

Figure 2 – Wild boar (*Sus scrofa*) seasonal relative abundance index (RAI) obtained at wallows, rubbing trees and random locations in central Croatia.

Wallowing was observed significantly ($p < 0.05$) more often in autumn than in spring and winter, and in summer than in spring (Fig. 3). Rooting was observed significantly ($p < 0.05$) more frequently in spring than in all other seasons. No significant differences were found for other seasonal comparisons (for all observed behaviours; see Tab. 1). Behaviour scored as "other" was not used in further analysis due to the small number of such events (less than 1 % in each season). Wild boar selected significantly more coniferous trees for rubbing than deciduous trees in all seasons ($p < 0.05$).

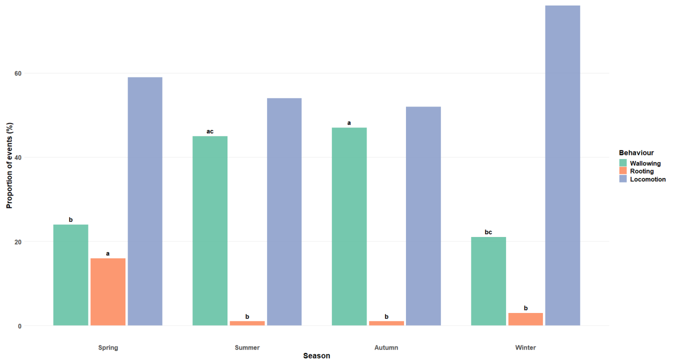

Figure 3 – Ratio of different wild boar (*Sus scrofa*) behaviours throughout different seasons captured with camera traps on wallows in central Croatia.

The activity level of wild boar did not differ significantly between the wallows and random locations ($p > 0.05$). However, the activity level at wallow locations was significantly lower in spring ($p < 0.05$) than in autumn and winter (Tab. 2). For both location types (wallow and random), activity was highest in autumn (Tab. 2).

Overlaps between the seasonal activity patterns of wallows and random locations by season are shown in Fig. 4. The seasonal activity patterns showed a high degree of overlap between the wallows and random locations throughout the year. The lowest overlap coefficient was observed in summer (0.79), which can be attributed to increased diurnal activity at the wallows. The highest overlap coefficients were observed in winter (0.93), followed by autumn (0.86), indicating a similar pattern of activity between the wallows and the random locations during these seasons. The overall overlap in activity patterns between wallows and random locations was 0.88.

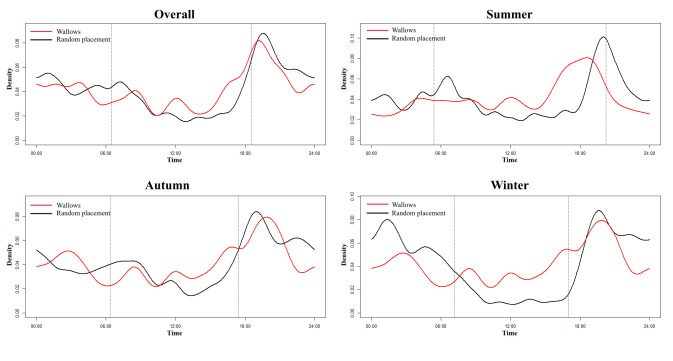

Figure 4 – Overlap of overall and seasonal wild boar (*Sus scrofa*) activity patterns obtained at wallows and random locations in central Croatia.

Regarding the activity pattern, the overall peak of activity at wallows and random locations was shortly after 6 p m In spring, the only peak of activity at the wallows was around 9 p m , with a similar activity level throughout the rest of the day (Fig. S5). In summer, the peak of activity at wallows was around 8 p m , and activity was lowest around midnight. In autumn, the highest activity was observed around 7 p m , and the lowest activity around noon for both setups. In winter, two activity peaks were observed, the first around 2 a m and the second around 7 p m , while the lowest activity was observed around midday for both experimental setups (Fig. 4).

Discussion

In the present study, RAI and seasonal patterns in wild boar behaviour and activity captured by camera traps at wallows, rubbing trees, and random locations were investigated. There were no differences in RAI at the wallows between seasons, and between locations during study period. RAI at random locations was significantly higher during summer. Wallowing was observed significantly more often during autumn in relation to spring and winter, and significantly more in summer than in spring. Rooting as behaviour was recorded significantly more during spring. Wild boar used significantly more coniferous trees for rubbing than deciduous trees. The activity level at wallows was lower in spring than in autumn and winter, while there were no differences in other comparisons (between seasons and between the wallows and random locations). The overlap coefficient between the wallows and random locations was lowest in summer, when wild boar activity was higher during the day. Different age and sex categories of wild boar used the wallows and rubbing trees (Fig. S6-S9).

Wild boar behaviour is the result of an interaction between intrinsic (energy production, reproduction) and extrinsic factors (habitat, climate, presence of predators) (Naguib, 2006; Morelle et al., 2014). Wallowing can be considered comfort behaviour, but can also have other important functions for wild boar (Bracke, 2011; Erdtmann and Keuling, 2020). Wild boar tend to use wallows throughout the year, regardless of season (Belden and Pelton, 1976). This was also supported by present study, when no significant differences in RAI were found between seasons, but high variance was observed between locations and within the same locations between seasons (Fig. 2). Spring seemed to be the predominant season in terms of RAI at wallows, closely followed by summer and autumn. Rooting had a significantly higher occurrence during spring than in other seasons, highlighting the foraging usage of wallows during spring. Krčmar (2019) investigated the abundance of different tick species across seasons in Croatia, and found that the highest abundance of all tick species was recorded in spring, suggesting that this increased abundance of ectoparasites in spring could also influence the use of wallows and rubbing trees by wild boar. According to Crouch (1983), wallows are utilised more frequently in the summer months. In summer, wallowing is important for thermoregulation, while in autumn it is part of mating behaviour (Bracke, 2011). Because the piglets are born during spring, RAI is expected to rise in spring and decrease gradually throughout the year, especially during winter, due to the intensive culling in the driven hunts. Even though RAI on wallows didn't differ significantly throughout the year, wallowing events were significantly more frequent in autumn and summer than spring, supporting a sexual and thermoregulatory role for wallows. During the mating season, sows and boars tend to leave taint in and around the wallows to mark their territory (Allwin et al., 2016). In the context of climate change, autumn has become warmer as a season, resulting in the wallow being used for thermoregulation over a longer period and overlapping with the mating season (Scandura et al., 2022; Calinger and Curtis, 2023). Since the results of the present study show that wallowing as a behaviour was observed significantly more often during autumn than in spring or winter, and significantly more in summer than in spring, it can be proposed that heat stress, especially in combination with mating season, has an impact on the occurrence of wallowing. Although not statistically significant, the difference between the obtained RAI at wallows and random locations is the highest during autumn, suggesting a possible preference for wallows during this season. Winter is the coldest season and the least favourable for wildlife, resulting in the lowest RAI values at the wallows. During this season, animals are less active to reduce energy loss and maintain optimal body temperature (Speers-Roesch et al., 2018; Guiden and Orrock, 2020)). Nevertheless, sows in late gestation also exhibit wallowing behaviour in winter (Buckner et al., 1998). Another explanation is that the incidence of ectoparasites is lowest in winter months (Krčmar, 2019), which also coincides with the lowest RAI at rubbing trees.

Locomotion as behaviour was more common (although not statistically significant) in winter than in other seasons. In winter, the peak of the mating season is over and wild boar do not need to wallow for

Table 2 – Activity level, number of animals and trapping effort of wild boar (*Sus scrofa*) during different seasons at wallows and random locations in central Croatia.

Variables	Season			
	Spring	Summer	Autumn	Winter
AL-wallows	0.38 ± 0.04^{a}	0.47 ± 0.04^{ab}	0.53 ± 0.04^{b}	0.51 ± 0.03^{b}
AL-random	–	0.41 ± 0.02	0.50 ± 0.02	0.47 ± 0.02
Animals[1] (N)	679	396	631	369
Independent events at wallows	235	193	255	188
Trapping effort at wallows	487	464	574	627

AL – activity level; [1]total number of observed animals at wallows; ^{a,b} values marked with different letters differ significantly ($p < 0.05$)

thermoregulation. In addition, microbiological activity in the soil is lower in cold weather and the soil may be frozen for certain periods (Pietikäinen et al., 2005). Therefore, it is expected that they will reduce the percentage of wallowing and rooting and increase the percentage of locomotion. Nevertheless, wild boar have been repeatedly observed to use the wallows during winter driven hunts, which can be associated with two behaviours: *i*) thermoregulatory behaviour (Vestergaard and Bjerg, 1996) to cool the body while running from hunting dogs, and *ii*) anti-predator behaviour (Gosling and McKay 1990) to conceal their scent and deceive the dogs (Šprem N., unpublished data). Therefore, wallowing can still be expected during winter, but not as much as during other seasons. In general, this behaviour was most evenly distributed over the seasons. Foraging behaviour in wild boar generally occurs in relatively small areas, over short distances, and with low locomotion speed (Spitz and Janeau, 1990; Morelle et al., 2015). Erdtmann and Keuling (2020) reported that behaviours such as foraging and locomotion are more common than wallowing. They found that rooting as a type of foraging behaviour had the highest frequency at wallows in spring, similar to the present study, as vegetation starts and the biological and microbiological activity of the forest soil is at its highest (Ugarković et al., 2011; Žifčáková et al., 2016). The lower frequency observed in summer can be attributed to high air and soil temperatures and dry soil conditions, which reduce food availability for omnivorous wild boar and hinder rooting behaviour due to increasing dryness (Ugarković et al., 2018; Ruf et al., 2021). In addition to foraging, rooting can also be observed in nest building or thermoregulation by facilitating access to cooler soil layers or helping to create wallows that help dissipate body heat at high ambient temperatures (Baert et al., 2022).

The highest activity level in autumn at wallows can be attributed to the mating season, while the lowest activity level in spring is due to farrowing. This is because sows look for safe places to nest before farrowing, away from disturbances (Saïd et al., 2012). Previously, sows were reported to reduce their activity about one month before farrowing (Morelle et al., 2015; Allwin et al., 2016), which is consistent with the lower activity level found in sows in spring at the wallows. At random locations, activity levels were also highest in autumn (mating season), followed by winter and summer. The increased activity in autumn and winter in the present study can also be attributed to human disturbance, i.e., the peak of the hunting season and frequent driven hunts (Thurfjell et al., 2013; Olejarz et al., 2024). Although research by Šprem et al. (2015) on chamois (*Rupicapra rupicapra*) confirmed that ungulate activity can be influenced by large carnivores, we believe that in the present study, large carnivores exert a lesser pressure than humans, as a lower number of individuals predated by wolves is expected, similar to the ratio reported by Bassi et al. (2020). Also, due to the scavenging behaviour of wild boar, wolves can provide additional food resources for wild boar with the carcasses of killed animals, thus increasing food availability and reducing activity (Brogi et al., 2025), which is not the case in our study. Therefore, the increase in wild boar activity during autumn and winter is related mostly to the mating season and human disturbance (peak of driven hunting season). The lowest activity level at random locations in summer can be attributed to less human disturbance, higher temperatures, and higher food availability (Johann et al., 2020; Greco et al., 2021).

Since the overlap coefficient between the activity patterns at the wallows and the random locations was lowest in summer and most activity occurred during the day, camera traps were left at the wallows in summer 2024 to verify whether the results of summer 2023 were an exception. The activity patterns recorded at the wallows during the 2023 and 2024 summer seasons overlapped strongly, with the same peak of activity at around 6 p m , and activity was diurnal (Fig. S9). According to the results of the random locations presented in this study, wild boar were most active at dusk and at night, mainly due to the maintenance of body temperature, i.e., thermoregulation (Allwin et al., 2016). Wild boar usually forages for food in the first half of the active period, while wallowing and other comfort behaviours occur during the other half (Keuling and Stier, 2009). In addition, in the present study, it was observed that wallowing activity occurred more frequently during the day and at dusk in summer, which is consistent with the findings of Mersinger and Silvy (2007) who concluded that the mean distance from free water in feral pigs is greater during night than during the day during summer.

To summarise, wild boar regularly use wallows, making the wallows well suited for camera trap monitoring, and provides an insight into the occurrence and activities of wild boar. Despite the fact that 94 warm days ($T_{max} > 25.0$ °C) and 32 hot days ($T_{max} > 30.0$ °C) were recorded in the study area during the year, especially in summer, the wild boar occurrence at the wallows was not different during this season. Given that the highest difference was recorded in autumn, we suggest that wallows gain additional significance during the mating season, supporting sexual function alongside their roles in thermoregulation and ectoparasite defence. Finally, camera traps at wallows can be used in combination with other available tools (such as environmental DNA diagnostics) for effective disease management and improved protection of wild boar and human health (Varzandi et al., 2024).

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Supplemental information

Additional Supplemental Information may be found in the online version of this article:

Table S1 Monitored trees that wild boar used for rubbing with seasonal number of trapping days and number of rubbing events.
Table S2 Measurements of monitored wallows.
Table S3 Model results.
Table S4 Model results- pairwise contrasts.
Figure S5
Figure S6
Figure S7
Figure S8
Figure S9
Figure S10