

Behavioural patterns of free roaming wild boar in a spatiotemporal context

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Although the almost worldwide distributed wild boar *Sus scrofa* is a well-studied species, little is known about the behaviour of autochthonous, free living wild boar in a spatiotemporal context which can help to better understand wild boar in conflict terms with humans and to find solutions. The use of camera traps is a favourable and non-invasive method to study them. To observe natural behaviour, 60 camera traps were placed for three months in a state forest of 17.8km² in the region of the Luneburg Heath in northern Germany. In this area wild boar, roe deer, red deer, wolves and humans are common. The cameras recorded 20 s length video clips when animals passed the detection zone and could be triggered again immediately afterwards. In total 38 distinct behavioural elements were observed, which were assigned to one of seven behavioural categories. The occurrence of the behavioural categories per day was evaluated to compare their frequencies and see which are more essential than others. Generalised Additive Models were used to analyse the occurrence of each behaviour in relation to habitat and activity time. The results show that essential behavioural categories like foraging behaviour, locomotion and vigilance behaviour occurred more frequently than behaviour that “just” served for the well-being of wild boar. These three behavioural categories could be observed together mostly in the night in broad-leaved forests with a herb layer of 50-100 %, comfort behaviour occurred mostly at the ponds in coniferous forest. It is also observable that the behavioural categories foraging and comfort behaviour alternated several times during the night which offers the hypothesis that foraging is mostly followed by comfort behaviour. These findings pave the way towards implementing effective control strategies in the wild and animal welfare in captivity.

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Abstract

Although the almost worldwide distributed wild boar *Sus scrofa* is a well-studied species, little is known about the behaviour of autochthonous, free living wild boar in a spatiotemporal context which can help to better understand wild boar in conflict terms with humans and to find solutions. The use of camera traps is a favourable and non-invasive method to study them. To observe natural behaviour, 60 camera traps were placed for three months in a state forest of 17.8 km² in the region of the Luneburg Heath in northern Germany. In this area wild boar, roe deer, red deer, wolves and humans are common. The cameras recorded 20 s length video clips when animals passed the detection zone and could be triggered again immediately afterwards. In total 38 distinct behavioural elements were observed, which were assigned to one of seven behavioural categories. The occurrence of the behavioural categories per day was evaluated to compare their frequencies and see which are more essential than others. Generalised Additive Models were used to analyse the occurrence of each behaviour in relation to habitat and activity time. The results show that essential behavioural categories like foraging behaviour, locomotion and vigilance behaviour occurred more frequently than behaviour that “just” served for the well-being of wild boar. These three behavioural categories could be observed together mostly in the night in broad-leaved forests with a herb layer of 50-100 %, comfort behaviour occurred mostly at the ponds in coniferous forest. It is also observable that the behavioural categories foraging and comfort behaviour alternated several times during the night which offers the hypothesis that foraging is mostly followed by comfort behaviour. These findings pave the way towards implementing effective control strategies in the wild and animal welfare in captivity.

Introduction

Animals behave in order to survive and reproduce themselves (Naguib 2006; Kappeler 2009) and choose different habitats to increase their survival and fitness. Behaviour is defined as control and exercise of movements or signals with which an animal interacts with conspecifics or other components of its animate and inanimate environment, as well as activities which serves for the homoeostasis of an individual (Kappeler 2009). Some animals within a given population, however, will perform much better in some habitats than in others (Gaillard et al. 2010). Within a day terrestrial herbivores relocate between foraging areas, drinking and resting sites and places used for other activities at different times of the day (Owen-Smith et al. 2010). Predation pressure, inter- and intraspecific competition, diseases and human disturbances can affect the behaviour and consequently the survival and fitness of animals (Gaillard et al. 2010). A first step to assess functions of a specific behaviour, and henceforth to analyse behaviour changes, is to watch the behavioural elements performed in specific places at defined times of the day to understand their benefits for survival.

Among the terrestrial even-toed ungulates (*Artiodactyla*) the Suina (Price et al. 2005; Gatesy 2009) is the only omnivorous non-ruminant suborder with several of original features (Briedermann 2009). Among the Suina the species *Sus scrofa* is distributed almost worldwide (Lowe et al. 2000; Briedermann 2009; Mayer 2009). Wild boar are amongst the most intelligent and adaptable large terrestrial mammals in Central Europe (Briedermann 2009) making it very interesting for behavioural analyses in relation to the time of day and different habitat types. Only few studies analysed the behaviour of wild boar under natural conditions (Allwin et al. 2016; Probst et al. 2017). Most studies were conducted at artificial feeding places (Schneider 1980; Saebel 2007; Focardi et al. 2015) or in enclosures (e.g. Gundlach 1968; Beuerle 1975;

Altmann 1989) which does not necessarily enable to cover all behavioural elements that would normally occur over the course of a day in a wild population. There is a lack of recent field studies under natural conditions due to the fact that wild boar are widely seen as a pest because of their constant conflict terms with humans, such as crop damage, disease transmission (Keuling et al. 2013; Allwin et al. 2016; Probst et al. 2017) and zoonosis, road traffic accidents, and disturbances to sensitive plant communities (Maselli et al. 2014). Though, it is very important to understand the behaviour of wild boar to be able to implement effective management strategies for reduction plans (Maselli et al. 2014) as well as for animal welfare in enclosures (Kovács et al. 2017).

As the behaviour of wild boar hardly differs from that of domestic pigs (Stolba and Wood-Gush 1989; GÖT and BAT 2003; Mayer 2009), their behaviour can be summarised by: resting, locomotion, behaviour caused by metabolism (ingestion and excretion), comfort, vigilance, social and sexual (Gundlach 1968; Beuerle 1975; Saebel 2007) (see Table 1). Most of the day (70-90%) is spend on foraging to fulfil the animals basic needs (Briedermann 1971; GÖT and BAT 2003; Keuling and Stier 2009), of which about half is filled by ingestion or locomotion (Stolba and Wood-Gush 1989; Morelle et al. 2014). Comfort behaviour, in contrast, is practised much less but serves the important function of well-being (Keuling and Stier 2009).

Wild boar, however, due to their intelligence and adaptability, can learn new attitudes due to training and imitation (Schneider 1980; Broom et al. 2009; Sommer et al. 2016). Studies show that the behaviour of wild boar differs depending on the region (habitat), population, and individual (Schneider 1980). For activity and habitat choice behaviour in particular, the same biotic and abiotic factors are important (Choquenot et al. 1996; Lemel et al. 2003; Briedermann 2009). In general, wild boar prefer broad-leaved forest with older mast species (beech, oak)

while foraging (Berger 2006; Bertolotto 2010) which they mainly explore in the first half of their activity time (Keuling and Stier 2009). In contrast, coniferous forest is preferred for their resting sites (Bertolotto 2010) as well as secure places for wallowing and sleeping (GÖT and BAT 2003; Keuling and Stier 2009; Allwin et al. 2016). Comfort behaviour often takes place in the second half of the night (Keuling and Stier 2009).

To fill the gap of authentic wild boar behaviour in a spatiotemporal context, we aimed to 1) reveal a myriad of behavioural elements of wild boar, and 2) relate functions to them depending to the spatiotemporal occurrence. The following hypotheses are tested: 1. Essential behavioural categories like foraging, vigilance and related locomotion occur more frequently than behaviour serving for the well-being of wild boar like comfort behaviour. 2. Foraging and other related behavioural categories occur in the first half of the night in broad-leaved forest, whereas comfort and related behavioural categories can be observed later in the night in coniferous forest or at places where the animals feel secure.

Materials and Methods

Study area

The study area “Süsing” was a 17.8 km² state forest located in the Luneburg Heath in Germany. The region is characterised by large-area coniferous forest (*Pinus sylvestris*, *Picea abies*, *Larix decidua* & *L. kaempferi*, *Pseudotsuga menziesii*) and small-area oak (*Quercus robur*) and beech (*Fagus sylvatica*) forests (Keuling et al. 2013). The mean annual temperature is 8 °C and the average annual rainfall is approximately 700 mm (Keuling et al. 2013). Besides a high number of

wild boar (about 8 animals/km² during the study period, calculated according to Rowcliffe via Random Encounter Model (REM) (Rowcliffe et al. 2008)), there are also high numbers of roe (*Capreolus capreolus*) and red deer (*Cervus elaphus*), as well as a few wolves (*Canis lupus*).

Data collection

Direct observations (compared to radio telemetry) are required to record the behaviour of animals and consequently also get information on activity and habitat choices (Cagnacci et al. 2010). One cost-efficient method for the observation of free roaming wild boar is the use of camera traps. The advantage of camera traps is that they are non-invasive (Rovero et al. 2010; Rowcliffe et al. 2011), and as a consequence, ideal to study nocturnal and crepuscular animals which avoid humans (Rovero et al. 2010). The technique is applicable to the study of wild boar given they rarely react to camera traps (Amelin 2014). Using ESRI® ArcGis 10.1, 50 random points separated by a minimum distance of 100 m (Rowcliffe et al. 2008; Rovero et al. 2013) were determined and afterwards explored with GPS (Rovero et al. 2010; Rowcliffe et al. 2011). Additionally ten places with a high probability of wild boar occurrence (e.g. wallows, fresh rooting places, salt lick) were selected to reveal all behavioural elements necessitated for the ethogram. Cameras were placed at all 60 places.

The set-up of the Bushnell® TROPHY CAM™ and Bushnell® TROPHY CAM HD™ camera traps took place on 03.03.2014. The 50 cameras used for statistically evaluable behaviour observations were hung as near as possible to the random points, at trees in 90 cm height, orientated parallel to the ground (Rowcliffe et al. 2011; Meek et al. 2012) to capture some open space on the video clips, and if possible, a deer crossing which comes to or goes away from the camera (Bengsen et al. 2011; Rowcliffe et al. 2011). The additional ten camera traps, which are

statistically irrelevant for the behaviour frequency, were hung at different heights depending on the area to capture a large field of view and thus a lot of behaviours. To not disturb the natural behaviour of the animals, no bait or lure were used at the random points (Rowcliffe et al. 2011; Meek et al. 2012). Each camera had a passive infrared sensor (PIR) and recorded, day and night, a 20 s video clip without sound when they were triggered. 1 s after the ending of the latest video the camera traps could be triggered again (Rovero et al. 2010; Rowcliffe et al. 2011). The video clips were stored on SD cards, which were changed biweekly. After about three months, on 04.06.2014, the camera traps were retrieved.

The date and time for each clip was recorded (the time is presented in segments as full hours with the following full hour, e.g. 00:00 o'clock = 00:00:00 - 00:59:59 o'clock).

The habitat was described at each of the camera locations. First, every place was assigned to one of the six types: track, forest aisle, pond (incl. wallows), field edge (simultaneously edge of the forest), salt lick or wooded. After that, the tree and shrub layer were described with main species (no trees/shrubs, broad-leaved, mixed or coniferous forest) and cover (0 %, 0-50 % or 50-100 %). The herb layer was also divided as described. Here the main species were no herbs, common bracken (P.a. = *Pteridium aquilinum*), European blueberry (V.m. = *Vaccinium myrtillus*), bracken and blueberry (P.a.&V.m.) or herbs (e.g. *Rubus* sectio *Rubus*, *Urtica dioica*, Poaceae, a few Cyperaceae and Polypodiopsida). In addition, the cover of deadwood (0 %, 0-25 % or 25-50 %) was registered.

In this study the sampling method “behaviour sampling” and the recording method “time sampling, one-zero sampling” (Altmann 1974; Geissmann 2002) were used. That means, during a sampling interval (video length of 20 s) all visible boar were observed as one group and it was noted for every behavioural element if it occurred in the video clip or not. An ethogram was

created following literature review (e.g. Gundlach 1968; Saebel 2007; Briedermann 2009) and own observations, at which exclusively the own observations are shown in Table 1. Due to the German law for animal welfare these non-invasive investigations are no subject to approval.

Data analysis

Wild boar could be identified on 1,227 of ca. 8,500 video clips as well as at 57 of 60 places. From 1,169 video clips, a behavioural context could be analysed (645 of 673 video clips at the random points, 524 of 554 video clips at the other ten places), but only the video clips at the random points were statistically analysed, because the other ten did not fulfil the statistical requirements (not randomly, hung at different heights).

To compare the occurrence per day of the seven different behavioural categories at the random points, two analyses were done: First, to calculate the percentage of each behavioural category, the number of observations per behavioural element (BE) and random point (RP) at one day was calculated as the function:

$$N_{\text{obs},d=1}(BE,RP) = \frac{N_{\text{obs}}(BE,RP)}{d_{RP}}$$

where $N_{\text{obs}}(BE,RP)$ is the total number of observations per behavioural element and random point and d_{RP} is the number of trial days per random point. Then the mean number of observations per behavioural element could be calculated by:

$$\bar{x}(BE) = \frac{\sum(N_{\text{obs},d=1}(BE,RP))}{50}$$

where 50 is the number of random points. The percentage for each behavioural category (BC) in % (with $\sum(P(BC)) = 1$) was then calculated by:

$$P(BC) = \frac{\sum_{(BC)}(\bar{x}(BE)) * 100}{\sum(\bar{x}(BE))}$$

where $\sum_{(BC)}(\bar{x}(BE))$ describes the sum of the mean numbers of observations per behavioural element over all behavioural elements, which belong to one behavioural category.

Second, to compare the occurrence of the behavioural categories, the number of observations per behavioural category and random point was calculated as the function:

$$N_{obs}(BC,RP) = \sum_{(BC,RP)}(N_{obs,d=1}(BE,RP))$$

where $\sum_{(BC,RP)}(N_{obs,d=1}(BE,RP))$ describes the sum of the numbers of observations per behavioural element and random point at one day over all behavioural elements, which belong to one behavioural category. Afterwards pairwise comparisons of means (over all random habitats) were conducted with RStudio V 0.98.978. Therefore, the linear mixed model (LMM) (Dormann and Kühn 2009) combined with the post hoc analysis least squares means (LSMEAN) (SAS Institute Inc. 2011) with Tukey adjustment (NIST/SEMATECH 2013) was performed.

For the analyses of the behaviour in a spatiotemporal context, similar behavioural elements were grouped as listed: locomotion; sniffing and winding; defecating and urinating; vigilance behaviour; rooting and pawing; salt ingestion; sucking attempt and suckling; chewing and feeding (attempt); drinking; wallowing, nibbling and stretching; shaking; rubbing; scratching (one's bottom) and rolling; social interactions; sexual behaviour (see Table 1). For each grouping the number of video clips per time of day was summed over all camera locations with Microsoft Excel 2007 to determine the activity maxima. Using the data from the random camera locations, a generalised additive model (GAM) dependent on the time of day and habitat type was calculated with RStudio V 0.98.978 for each behaviour with greater than 20 observations. Significant habitat preferences per behaviour were derived. Since it is not possible to monitor the

whole study area completely and consequently every possible habitat type, we can just draw conclusions out of the results given by random placed camera traps.

Results

Comparing the proportion of the six observed behavioural categories at the 50 random points, locomotion was observed in more than half of the video clips (52 %). This behaviour occurred significantly more often than all other behavioural categories (Fig. 1, LMM & LSMEAN see Table 2). It was followed by olfactory (22.02 %), vigilance (13.33 %) and foraging behaviour (8.81 %). The olfactory behaviour occurred significantly more often than foraging behaviour and comfort behaviour as well as social interactions. Vigilance behaviour occurred significantly more often than comfort behaviour and social interactions. Comfort behaviour (1.99 %) and social interactions (1.85 %) were rarely observed. There were no significant differences between all other pairwise comparisons.

The ten additional cameras were not used for habitat statistics but for general descriptions (i.e. salt ingestion). The observed wild boar are crepuscular and nocturnal because their main activity was between 17:00 and 08:59 o'clock. The activity maxima of locomotion occurred in the hour of 22:00 o'clock and in the hour of 03:00 o'clock. During this time the wild boar significantly avoided tracks and significantly preferred forest aisles, ponds and broad-leaved forest with 50-100 % herbs and 25-50 % deadwood (GAMs see S1 Appendix).

The highest activity maximum of sniffing and winding (olfactory behaviour) was between 20:00 and 21:59 o'clock and a secondary maximum in the hour of 03:00 o'clock. During this time the

wild boar avoided tracks and habitats with a shrub layer out of coniferous forest (GAMs see S1 Appendix). Ponds and habitats with 50-100 % herbs and 25-50 % deadwood were significantly preferred. Data show no obvious tendency for defecating and urinating.

The vigilance behaviour had an activity maximum at 22:00 o'clock and a secondary maximum at 03:00 o'clock. During this time wild boar significantly preferred forest aisles, ponds, a tree layer out of broad-leaved and mixed forest, a shrub layer out of broad-leaved forest, a herb layer with a cover of 50-100 % and 25-50 % deadwood (GAMs see S1 Appendix).

The foraging behaviour had an activity maximum at 17:00 o'clock for salt ingestion, which only occurred at the salt lick, and for chewing and feeding (attempt), which occurred significantly more often at ponds and places with a shrub cover of 50-100 % and blueberries (GAMs see S1 Appendix). At 19:00 o'clock, there was a secondary maximum again for chewing and feeding (attempt). In the hour of 21:00 o'clock a maximum of salt ingestion and for water intake (only at ponds) was observed. Another maximum occurred at 22:00 o'clock for sucking attempt and suckling, which mostly occurred at the ponds and at the salt lick, and for rooting and pawing. Pawing could significantly be observed at forest aisles, ponds and broad-leaved forest with herbs (GAMs see S1 Appendix). At 03:00 o'clock there was another maximum for rooting and pawing and in the hour of 04:00 and 06:00 o'clock again two low secondary maxima for chewing and feeding (attempt).

The comfort behaviour showed a secondary maximum for shaking in the hour of 17:00 o'clock at the salt lick. Furthermore, at around 20:00 o'clock there was a maximum for all elements of comfort behaviour, e.g. for shaking, which mostly occurred at the ponds this time. Another secondary maximum was in the hour of 23:00 o'clock for wallowing, mostly followed by rubbing, nibbling and stretching, which occurred only at the ponds. In the hour of 00:00 o'clock

there was a secondary maximum for scratching (one's bottom) and rolling, in which scratching often occurred at the ponds while rubbing.

The social interactions had a low maximum (compared to the size of the maxima of the other behavioural categories) in the hour of 20:00 o'clock. In general, this behavioural category occurred more often in the first half of the night with preferred habitats of forest aisles, ponds, a shrub layer out of 0-50 % broad-leaved and mixed forest, herbs and 25-50 % deadwood (GAMs see S1 Appendix). The sexual behaviour only occurred once at the salt lick in the hour of 20:00 o'clock.

For the several activity maxima per behavioural category in total, the olfactory behaviour occurred mostly in the hour of 20:00 o'clock in form of winding at a rubbing tree during comfort behaviour, in the hour of 21:00 o'clock in form of winding at the salt lick during salt ingestion and in the hour of 03:00 o'clock in form of sniffing on the ground during rooting (Fig. 2).

Furthermore, foraging behaviour and comfort behaviour alternated during the night. After awakening, wild boar first attended to foraging behaviour between 17:00 and 19:59 o'clock, followed by a short maximum of comfort behaviour in the hour of 20:00 o'clock. Afterwards, between 21:00 and 22:59 o'clock, the animals again attended to foraging behaviour until a longer period of comfort behaviour can be observed between 23:00 and 01:59 o'clock. To a minor degree, the rest of the night (02:00-08:59 o'clock) is used for foraging behaviour.

Discussion

During the observation of wild boar with camera traps, 38 behavioural elements were observed in this study which could be combined into seven behavioural categories. The behavioural

category locomotion occurred the most in this study, followed by olfactory, vigilance and foraging behaviour. In many other studies (e.g. Stolba and Wood-Gush 1989; GÖT and BAT 2003; Saebel 2007) foraging behaviour was the most observed behavioural category. A reason for this might be that in these studies locomotion was always analysed in its pure form and not when it occurred together with other behavioural categories like foraging behaviour (Briedermann 1971). Another reason might be that in our study the duration of the different behavioural categories were not measured. It is also possible that other studies counted sniffing for food as foraging behaviour, which was also often seen in this study. It is important to note, however, that related studies focused on domestic pigs (e.g. Stolba and Wood-Gush 1989; GÖT and BAT 2003; Mayer 2009), wild boar living in enclosures (e.g. Gundlach 1968; Beuerle 1975; Altmann 1989) or observed at feeding places (e.g. Schneider 1980; Saebel 2007; Focardi et al. 2015) and hence might show difference to behaviour in the wild. Wild boar in this study spent more time to foraging then undertaking comfort-related behaviour. According to other studies personal hygiene contributes less to the basic need of wild boar compared to foraging, because the latter serves to ensure survival and personal hygiene “just” for well-being (Saebel 2007; Keuling and Stier 2009). Consequently, our results and that from other studies confirm the hypothesis that behavioural categories, which are essential for survival like locomotion, vigilance and foraging behaviour, occur more often than categories serving for the well-being. Since olfactory behaviour occurred together with essential behaviour and those serving for the well-being it is not clearly assigned to one of them.

Behaviour in a spatiotemporal context

The maxima of locomotion and vigilance behaviour were observed with foraging behaviour (Fig. 2). Wild boar have to travel long distances while foraging and often have to cross open and unsecure spaces (Meynhardt 1982; Cahill et al. 2003), hence vigilance behaviour to avoid predators is important. Meanwhile the observed wild boar mostly used forest aisles or stayed in broad-leaved forests with a herb layer of 50-100 %. In other studies it was found that wild boar preferred broad-leaved forest for foraging (Berger 2006; Bertolotto 2010). Wild boar move fast and take the shortest path when crossing an open unsecure space (Meynhardt 1982). Manmade forest aisles that are rarely used by humans are probably used by wild boar (Allwin et al. 2016) to allow fast movement through forest areas. Thus, the hypothesis that foraging and related behaviour occur in broad-leaved forest is confirmed.

Social interactions and the only observation of sexual behaviour occurred during the maximum of comfort behaviour. This may be because comfort behaviour (Saebel 2007) and social interactions could be observed mostly at the ponds (containing wallows) where the animals feel safe (Keuling and Stier 2009). In addition, all ponds were located in coniferous forest, and wild boar prefer pine trees for rubbing (Mayer 2009). Furthermore, these three behavioural categories could be observed many times at the saltlick. In general, however, nearly all of the seven behavioural categories could be observed at the ponds. Consequently, the hypothesis that comfort and related behaviour occur in coniferous forest and at places where the wild boar feel safe cannot be rejected.

If we compare the alternation of foraging and comfort behaviour during the night with the results of another study (Gundlach 1968), the observations of the other study lack the first period of foraging behaviour after awakening and they also refer to diurnal wild boar. Our data support the results of other studies (Saebel 2007; Keuling and Stier 2009) which found that wild boar mostly

attend to foraging behaviour in the first half of the night while a higher occurrence of comfort behaviour during the second half of the night is not obvious. It rather gives the impression that foraging is always followed by comfort behaviour. Consequently, comfort behaviour occurs later in the night than foraging behaviour.

Functions of the behavioural elements

The behaviour of an animal essentially contributes to its survival and reproductive success (Naguib 2006; Kappeler 2009). If we generalise the ecological model for the locomotion of wild boar (Morelle et al. 2014), it appears that the behaviour of wild boar is a result of the interaction of intrinsic (energy gain, escape from predators and/or conspecifics, reproductive success) and extrinsic (habitat, climate, presence of predators) factors - and thus, it is the struggle of wild boar with its biotope (Naguib 2006). Our study supports this hypothesis. Further, we distinguished between basic animal behaviour serving the survival of the individuals and the sounder, and comforting behaviour aimed at the well-being of the individuals.

Our data supports, that wild boar use different behavioural elements for reaching different food resources. For example, rooting and pawing serve for the exposing of food sources in the ground (GÖT and BAT 2003). Wild boar can distinguish between food places of different quality and relocate them which saves energy and time (Held et al. 2005). Moreover, sows suckle their offspring and therefore invest in the breeding and survival of their offspring (Vetter et al. 2016). Our results show, that the functions of different behavioural elements are closely related. Wild boar, for example, have a very developed sense of smell (Graves 1984; Mayer 2009). The olfactory behaviour serves for foraging and avoidance of predators (sniffing and winding) as

well as for intraspecific communication by defecating and urinating. Also rubbing, nibbling as well as nose-to-nose contact and nose-to-body contact serve for intraspecific communication.

Vigilance behaviour (pausing) seemed to be a reaction to the camera traps. Our results show that wild boar, compared to other animals, hardly react to camera traps, but when they react, they do it by eye-contact or pausing (Amelin 2014). Wild boar are reclusive animals (Gundlach 1968; Beuerle 1975; Altmann 1989). Vigilance behaviour is used by wild boar to avoid predation (e.g. by humans or wolves), for example when a sow guards a glade before other sows and young animals follow her. When pausing or laying down, the movement is abruptly stopped which otherwise would produce a noise, which predators could hear. Moreover, young boar are very camouflaged while laying down due to their striped pattern (Briedermann 2009). The animals also use this moment to scan their environment multisensory (Quenette and Desportes 1992). If the boar do not find the source of the noise or sense disturbing them, it could be that they react with flight.

The behavioural category comfort behaviour mostly serves for two functions, personal hygiene behaviour and resting behaviour. Looking at the personal hygiene behaviour, wild boar use wallowing for thermoregulation because they are not able to sweat and a mud layer also keeps stinging insects away (Meynhardt 1982; GÖT and BAT 2003; Briedermann 2009). According to another study, wild boar immobilise stinging insects with help of the mud and afterwards remove them by rubbing and similar behaviour (Mayer 2009). Rubbing is also caused by hair change in spring-time (Briedermann 1971). Thus, comfort behaviour serves for the well-being of the animals in general (GÖT and BAT 2003). In contrast to the results of previous studies, where stretching was always observed after resting behaviour (Briedermann 2009), in our study stretching also could be seen three times mostly after rubbing and before shaking.

The social interactions of wild boar have different functions. Nose-to-nose contact and nose-to-body contact serve as intraspecific communication (see above). This is important for the mother-infant-relationship (Gundlach 1968; Meynhardt 1982), and for sexual behaviour (e.g. courtship of boars, boar fights), which serves for reproduction. It is said that each behaviour is noticed by group members and has social consequences (Stolba and Wood-Gush 1989), allowing them to learn from each other (Schneider 1980; Briedermann 2009; Morelle et al. 2014). Young boar train from an early age on fighting and copulation in a playful manner (Gundlach 1968; Meynhardt 1982; GÖT and BAT 2003), which they use later during the mating season for boar fights and mating. Wild boar also compete for food, however, they have a stable food hierarchy (Beuerle 1975; GÖT and BAT 2003; Saebel 2007) to avoid unnecessary competition and to save energy.

Resting behaviour like sleeping was not observed in this study. Wild boar rest at their daytime resting sites (Gundlach 1968; Meynhardt 1982) which were never placed in front of any of the 60 camera traps. As wild boar prefer dense vegetation for their resting places (Allwin et al. 2016) it is statistically unlikely to catch such places randomly, since the camera traps need some open space to work correctly (cf. data collection). Again, we also do not know any resting place of wild boar in our study area, consequently it was not possible to place one of the 10 other camera traps at their daytime resting sites. To analyse this behaviour in following studies we suggest permanently placing recording video systems at preferred resting sites which should be determined before with help of telemetry (Lampe 2004; Sándor et al. 2014). Since our results stem only from videos in forest habitats, a lack of observations from open areas may explain lacks of activity maxima in the hour of 18:00 o'clock and between 01:00 and 02:59 o'clock, because at that time the wild boar were probably on greens, fields or at baiting stations (in

surroundings of private hunting grounds) for foraging. Another possibility is that the animals had an activity break between 01:00 and 02:59 o'clock in which time resting behaviour could have been observable. It has already been suggested that free roaming wild boar have a rest period in the second half of the night (Briedermann 1971), diurnal wild boar around midday respectively (Allwin et al. 2016).

In order to increase the chance for documentation of rare behaviours, further studies should be conducted in which more camera traps are placed, as several behaviours could not be observed in this study due to the biotope (habitat) of animals. Furthermore, mating and mating-related fights of males take place from November till January (Meynhardt 1982; Altmann 1989; Briedermann 2009) which is beyond the observation season. The season also has an influence on biotope choice (Keuling et al. 2009). Thus in future studies, it would be advisable to observe wild boar for at least one year via camera traps to get a whole impression of their spatiotemporal behaviour. This year long observation would also account for possible weather influences on the activity and habitat choice of wild boar (Saebel 2007; Briedermann 2009; Allwin et al. 2016). Sound recordings could, hence, be taken when looking at courtship interactions to record communication behaviour and to eliminate the influence of the data collection via camera traps.

Currently, the numbers of wolves are rising across Europe (Randi 2011; Arbieu et al. 2019) and hence, likely influence the behaviour of wild boar, like they do in other species, e.g. roe deer (Bongi et al. 2008) and alpine ibex (Grignolio et al. 2019). This study can serve as a baseline study to record behavioural changes of wild boar in areas in which apex predators are recurring and increasing. To see if the spatiotemporal behaviour changes, future studies could compare different study areas (including or excluding predators, hunting and other human impact, different habitats, different seasons during some consecutive total years).

Video traps are a good method to observe the behaviour of animals (Focardi et al. 2015) under natural conditions (Maselli et al. 2014; Probst et al. 2017). Although video traps are not always reliably triggered by wild boar (Amelin 2014), using a high number of them gives an effective alternative compared to telemetry which would require wild boar disturbing direct observations. In further studies it would be advisable to observe wild boar year round with additional sound recordings to get an overall impression of the wild boar behavioural repertoire and to increase the chance of detecting rare behaviours as well as behavioural changes due to human or recurring large predator impacts.

Conclusion

The behaviour of wild boar is a result of the interaction of intrinsic and extrinsic factors - and thus, it is the struggle of wild boar with its biotope. Essential behavioural categories like foraging behaviour, locomotion and vigilance behaviour occurred more frequently than behaviour “just” serving for the well-being of wild boar. Accordingly, the activity maxima of these three behavioural categories could be observed at the same time of the night, mostly in the hour of 22:00 and 03:00 o’clock in broad-leaved forests with a herb layer of 50-100 %, whereas comfort behaviour occurred mostly in the hour of 20:00 o’clock and between 23:00 and 00:59 o’clock at the ponds in coniferous forest. Foraging behaviour was observed predominantly in the first half of the night and alternated several times during the night with comfort behaviour. It gives the impression that foraging is always followed by comfort behaviour. Olfactory behaviour occurred together with essential behaviour and those serving for the well-being and is not clearly assigned to one of them. The results of this study are an important contribution towards wild boar control and welfare.

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References

- Allwin B, Swaminathan R, Mohanraj A, Suhas GN, Vedaminckam S, Gopal S, Kumar M (2016) The Wild Pig (*Sus scrofa*) Behavior - A Retrospective Study. Journal of Veterinary Science Technology 7. doi: 10.4172/2157-7579.1000333.
- Altmann D (1989) Sozialverhalten und Revierverteidigung in Beziehung zur Tageszeit beim Wildschwein, *Sus scrofa* L. Beiträge zur Jagd- und Wildforschung 16:202–211.
- Altmann J (1974) Observational study of behavior: Sampling methods. Behaviour 69:227–267.
- Amelin M (2014) Analyse von Auslösefehlern bei Wildkameras mittels Videoüberwachung und Reaktion von Wildtieren auf Infrarotblitze. B. Sc. Thesis, Gottfried Wilhelm Leibniz Universität Hannover.
- Arbieu U, Mehring M, Bunnefeld N, Kaczensky P, Reinhardt I, Ansorge H, Böhning-Gaese K, Glikman JA, Klut G, Nowak C, Müller T (2019) Attitudes towards returning wolves (*Canis lupus*) in Germany: Exposure, information sources and trust matter. Biological Conservation 234:202–210. doi: 10.1016/j.biocon.2019.03.027.
- Bengsen AJ, Leung LK-P, Lapidge SJ, Gordon IJ (2011) Using a general index approach to analyze camera-trap abundance indices. The Journal of Wildlife Management 75:1222–1227. doi: 10.1002/jwmg.132.
- Berger K (2006) Winterhabitatnutzung dreier subadulter, männlicher Wildschweine (*Sus scrofa* L.) im Pfälzerwald. D. Thesis, Albert-Ludwigs-Universität Freiburg.

- Bertolotto E (2010) Behavioural ecology of wild boar (*Sus scrofa*) in an Apennine environment. Ph. D. Thesis, University of Sassari, Italy.
- Beuerle W (1975) Freilanduntersuchungen zum Kampf- und Sexualverhalten des europäischen Wildschweines (*Sus scrofa* L.). Zeitschrift für Tierpsychologie 39:211–258.
- Bongi P, Ciuti S, Grignolio S, Del Frate M, Simi S, Gandelli D, Apollonio M (2008) Anti-predator behaviour, space use and habitat selection in female roe deer during the fawning season in a wolf area. Journal of Zoology. doi: 10.1111/j.1469-7998.2008.00481.x.
- Briedermann L (2009) Schwarzwild: Neuausgabe bearbeitet von Burkhard Stöcker. Kosmos, Stuttgart.
- Briedermann L (1971) Ermittlungen zur Aktivitätsperiodik des Mitteleuropäischen Wildschweines (*Sus s. scrofa* L.). Der Zoologische Garten N.F., Leipzig 40:302–327.
- Broom DM, Sena H, Moynihan KL (2009) Pigs learn what a mirror image represents and use it to obtain information. Animal Behaviour 78:1037–1041. doi: 10.1016/j.anbehav.2009.07.027.
- Cagnacci F, Boitani L, Powell RA, Boyce MS (2010) Animal ecology meets GPS-based radiotelemetry: a perfect storm of opportunities and challenges. Philosophical Transactions of the Royal Society B 365:2157–2162. doi: 10.1098/rstb.2010.0107.
- Cahill S, Llimona F, Gràcia J (2003) Spacing and nocturnal activity of wild boar *Sus scrofa* in a Mediterranean metropolitan park. Wildlife Biology 9:3–13.
- Choquenot D, McIlroy J, Korn T (1996) Managing vertebrate pests: Feral pigs. Bureau of Resource Sciences, Australian Government Publishing Service, Canberra.
- Dormann CF, Kühn I (2009) Angewandte Statistik für die biologischen Wissenschaften, 2nd edn. Helmholtz Zentrum für Umweltforschung-UFZ.
- Focardi S, Morimando F, Capriotti S, Ahmed A, Genov P (2015) Cooperation improves the access of wild boars (*Sus scrofa*) to food sources. Behavioural Processes 121:80–86. doi: 10.1016/j.beproc.2015.10.019.
- Gaillard J-M, Hebblewhite M, Loison A, Fuller M, Powell R, Basille M, Van Moorter B (2010) Habitat-performance relationships: finding the right metric at a given spatial scale. Philosophical Transactions of the Royal Society B 365:2255–2265. doi: 10.1098/rstb.2010.0085.
- Gatesy J (2009) Whales and even-toed ungulates (Cetartiodactyla). In: Hedges SB, Kumar S (eds) The timetree of life. Oxford University Press, pp 511–515.
- Geissmann T (2002) Verhaltensbiologische Forschungsmethoden. Eine Einführung. Schöningh Verlag, Münster.
- Gesellschaft für Ökologische Tierhaltung e.V. (GÖT), Verein Beratung artgerechter Tierhaltung e.V. (BAT) (2003) Verhalten, artgerechte Haltungssysteme und Stalleinrichtungen für Rind, Schwein und Huhn. Schlussbericht (Teil II) an das Bundesministerium für Ernährung, Landwirtschaft und

- Verbraucherschutz im Rahmen des Bundesprogramms Ökologischer Landbau 30–32.
- Graves HB (1984) Behavior and ecology of wild and feral swine (*Sus Scrofa*). Journal of Animal Science 58:482–492.
- Grignolio S, Brivio F, Sica N, Apollonio M (2019) Sexual differences in the behavioural response to a variation in predation risk. Ethology 125:603–612. doi: 10.1111/eth.12887.
- Gundlach H (1968) Brutfürsorge, Brutpflege, Verhaltensontogenese und Tagesperiodik beim Europäischen Wildschwein (*Sus scrofa* L.). Zeitschrift für Tierpsychologie 25:955–995.
- Held S, Baumgartner J, KilBride A, Byrne RW, Mendl M (2005) Foraging behaviour in domestic pigs (*Sus scrofa*): remembering and prioritizing food sites of different value. Animal Cognition 8:114–121. doi: 10.1007/s10071-004-0242-y
- Kappeler P (2009) Verhaltensbiologie, 2nd edn. Springer, Berlin, Heidelberg.
- Keuling O, Herbst C, Daim A, Siebert U (2013) Schwarzwildbewirtschaftung im Hochwildring Süsing. Jahresbericht 2012 an das Niedersächsische Ministerium für Ernährung, Landwirtschaft, Verbraucherschutz und Landesentwicklung. Stiftung Tierärztliche Hochschule Hannover.
- Keuling O, Stier N (2009) Schwarzwild - Untersuchungen zu Raum- und Habitatnutzung des Schwarzwildes (*Sus scrofa* L. 1758) in Südwest-Mecklenburg unter besonderer Berücksichtigung des Bejagungseinflusses und der Rolle älterer Stücke in den Rotten. Abschlussbericht 2002-2006 an die Oberste Jagdbehörde im Ministerium für Landwirtschaft, Umwelt und Verbraucherschutz Mecklenburg-Vorpommern und die Stiftung „Wald und Wild Mecklenburg-Vorpommern“. Technische Universität Dresden.
- Keuling O, Stier N, Roth M (2009) Commuting, shifting or remaining? Different spatial utilisation patterns of wild boar *Sus scrofa* L. in forest and field crops during summer. Mammalian Biology 74:145–152. doi: 10.1016/j.mambio.2008.05.007.
- Kovács V, Újváry D, Szemethy L (2017) Availability of camera trapping for behavioural analysis: An example with wild boar (*Sus scrofa*). Applied Animal Behaviour Science 195:112–114. doi: 10.1016/j.applanim.2017.05.019.
- Lampe T (2004) Wie Sau sich bettet - über die Wahl der Schlafplätze bei Wildschweinen (*Sus scrofa*). D. Thesis, Universität Bielefeld.
- Lemel J, Truvé J, Söderberg B (2003) Variation in ranging and activity behaviour of European wild boar *Sus scrofa* in Sweden. Wildlife Biology 9:29–36.
- Lowe S, Browne M, Boudjelas S, De Poorter M (2000) 100 of the world's worst invasive alien species: A selection from the Global Invasive Species Database. The Invasive Species Specialist Group (ISSG) a specialist group of the Species Survival Commission (SSC) of the World Conservation Union (IUCN).

- Maselli V, Rippa D, Russo G, Ligrone R, Soppelsa O, D'Aniello B, Raia P, Fulgione D (2014) Wild boars' social structure in the Mediterranean habitat. *Italian Journal of Zoology* 81:610–617. doi: 10.1080/11250003.2014.953220.
- Mayer JJ (2009) Biology of wild pigs: Wild pig behavior. In: Mayer JJ, Brisbin ILJ (eds) *Wild pigs: Biology, damage, control techniques and management*. Savannah River National Laboratory, Aiken, South Carolina, pp 77–104.
- Meek P, Ballard G, Fleming P (2012) *An introduction to camera trapping for wildlife surveys in Australia*. Invasive Animals Cooperative Research Centre, Canberra.
- Meynhardt H (1982) *Schwarzwild-Report: Mein Leben unter Wildschweinen*, 7th edn. Neumann-Neudamm, Leipzig, Radebeul.
- Morelle K, Podgórski T, Prévot C, Keuling O, Lehaire F, Lejeune P (2014) Towards understanding wild boar *Sus scrofa* movement: a synthetic movement ecology approach. *Mammal Review*. doi: 10.1111/mam.12028.
- Naguib M (2006) *Methoden der Verhaltensbiologie*. Springer, Berlin, Heidelberg.
- NIST/SEMATECH (2013) E-Handbook of Statistical Methods: 7.4.7.1. Tukey's method. In: US Department of Commerce. <http://www.itl.nist.gov/div898/handbook/prc/section4/prc471.htm>.
- Owen-Smith N, Fryxell JM, Merrill EH (2010) Foraging theory upscaled: the behavioural ecology of herbivore movement. *Philosophical Transactions of the Royal Society B* 365:2267–2278. doi: 10.1098/rstb.2010.0095.
- Price SA, Bininda-Emonds ORP, Gittleman JL (2005) A complete phylogeny of the whales , dolphins and even-toed hoofed mammals (Cetartiodactyla). *Biological Reviews* 80:445–473. doi:10.1017/S1464793105006743.
- Probst C, Globig A, Knoll B, Conraths,FJ, Depner,K (2017) Behaviour of free ranging wild boar towards their dead fellows: potential implications for the transmission of African swine fever. *Royal Society Open Science* 4. doi: 10.6084/m9.figshare.c.3780125.
- Quenette PY, Desportes JP (1992) Temporal and sequential structures of vigilance behavior of wild boars (*Sus scrofa*). *Journal of Mammalogy* 73:535–540.
- Randi E (2011) Genetics and conservation of wolves *Canis lupus* in Europe. *Mammal Review* 41:99–111. doi: 10.1111/j.1365-2907.2010.00176.x.
- Rovero F, Tobler M, Sanderson J (2010) Camera trapping for inventorying terrestrial vertebrates. In: Eymann J, Degreef J, Häuser C, Monje JC, Samyn Y, van den Spiegel D (eds) *Manual on field recording techniques and protocols for All Taxa Biodiversity Inventories and Monitoring*. The Belgian National Focal Point to the Global Taxonomy Initiative, pp 100–128.
- Rovero F, Zimmermann F, Berzi D, Meek P (2013) “Which camera trap type and how many do I need?”

A review of camera features and study designs for a range of wildlife research applications. *Hystrix*, the Italian Journal of Mammalogy 24:148-156. doi: 10.4404/hystrix-24.2-8789.

Rowcliffe JM, Carbone C, Jansen PA, Kays R, Kranstauber B (2011) Quantifying the sensitivity of camera traps: An adapted distance sampling approach. *Methods in Ecology and Evolution* 2:464–476.

Rowcliffe JM, Field J, Turvey ST, Carbone C (2008) Estimating animal density using camera traps without the need for individual recognition. *Journal of Applied Ecology* 45:1228–1236.

Saebel J (2007) Verhaltensbeobachtungen am Schwarzwild (*Sus scrofa* L.) durch Videoüberwachung und Radiotelemetrie. D. Thesis, Technische Universität Dresden.

Sándor G, Tari T, Heffenträger G, Pócza G, Náhlik A (2014) Daytime habitat use of wild boar. [Abstract] In: 10th International Symposium on Wild Boar and other Suids. Velenje, Slovenia (01.-05.09.2014).

SAS Institute Inc. (2011) SAS/STAT® 9.3 User's Guide. SAS Institute Inc., Cary, North Carolina.

Schneider E (1980) Markierung und Inbesitznahme von Futter, Nachahmung und Lernen beim europäischen Wildschwein (*Sus scrofa* L.). *Zeitschrift für Jagdwissenschaft* 26:126–132.

Sommer V, Lowe A, Dietrich T (2016) Not eating like a pig: European wild boar wash their food. *Animal Cognition* 19:245–249. doi: 10.1007/s10071-015-0903-z.

Stolba A, Wood-Gush DGM (1989) The behaviour of pigs in a semi-natural environment. *Animal Production* 48:419–425. doi: 10.1017/S0003356100040411.

Vetter SG, Brandstätter C, Macheiner M, Suchentrunk F, Gerritsmann H, Bieber C (2016) Shy is sometimes better: personality and juvenile body mass affect adult reproductive success in wild boars, *Sus scrofa*. *Animal Behaviour* 115:193–205. doi: 10.1016/j.anbehav.2016.03.026.

Table 1. Ethogram for the classification and definition of the behavioural elements of the observed wild boar.

Table 2. Results of the LMM and LSMEAN. Comparison of the occurrence of each behavioural category with each other. The estimate and p-value of each pairwise comparison of means with Tukey adjustment is shown.

Figure 1. Occurrence of the behavioural categories at the random points.

The mean number of videos clips per day is shown for the six behavioural categories (L = locomotion, OB = olfactory behaviour, VB = vigilance behaviour, FB = foraging behaviour, CB = comfort behaviour, SI = social

interaction) as box plots with minimum, lower quantile, median, upper quantile, maximum and outlier, observed at the random points (N = 1407; 645 videos clips).

Figure 2. Activity maxima per behavioural category.

A visual summary of the results is shown for all seven behavioural categories with maxima (= two frequency peaks), secondary (= one frequency peak) and low maxima (a half frequency peak, respectively a tenth frequency peak for sexual behaviour) (with e.g. 00:00 = 00:00-00:59) (N = 1227).

Supporting Information

S1 Appendix. Significant results of the GAM ($N > 20$).

S2 File. Data sets.

Figure 1

Occurrence of the behavioural categories at the random points.

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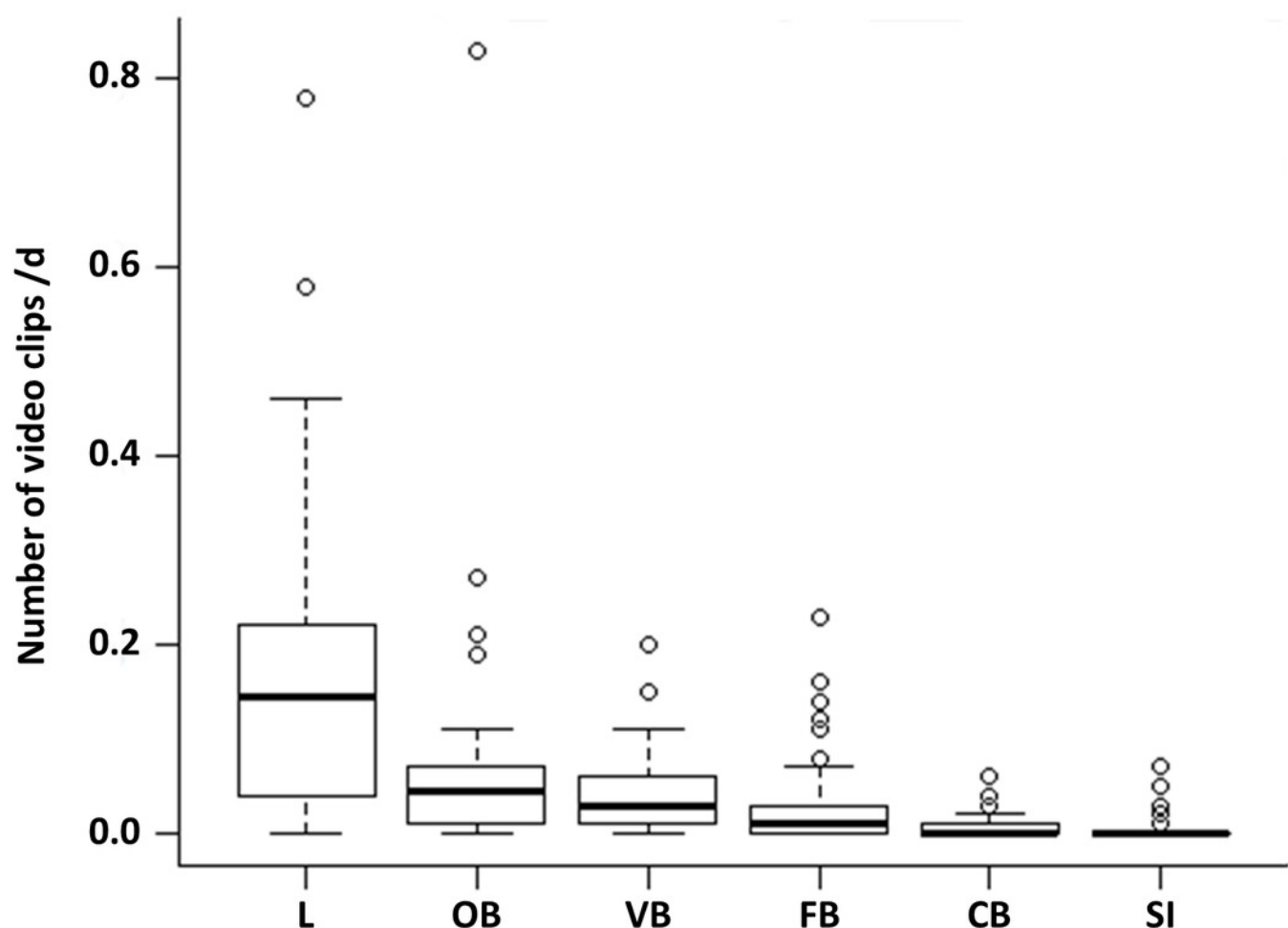


Figure 2

Activity maxima per behavioural category.

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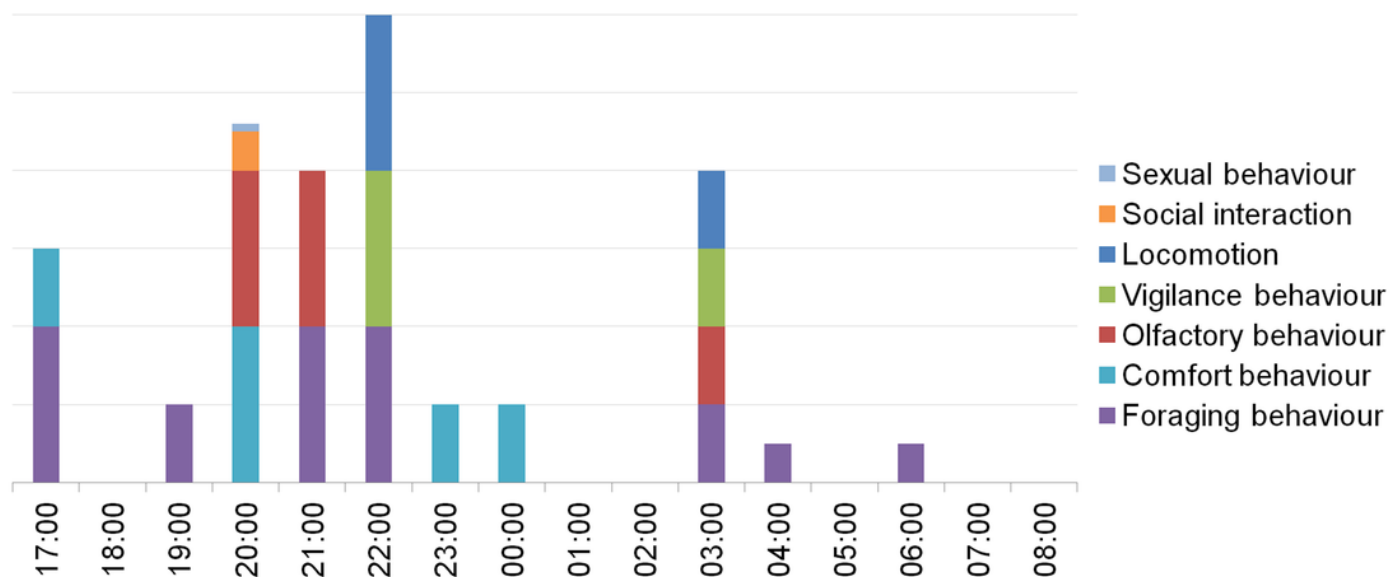


Table 1 (on next page)

Ethogram for the classification and definition of the behavioural elements of the observed wild boar.

1 **Table 1. Ethogram for the classification and definition of the behavioural elements of the observed wild boar.**

2

Context	Definition
Locomotion (L)	
Walking	Slow movement (pace), every leg is moved at least one step (also backwards possible).
Running	Fast movement (trot and faster).
Jumping	Jump over an obstacle or ditch.
Flight	Abrupt escape from recent whereabouts (optionally just a few steps).
Olfactory behaviour (OB)	
Sniffing	Sniffing on the ground or between plants of the ground and herb layer.
Winding	Sniffing in the air or at something (e.g. rubbing tree, camera).
Defecating	Emptying of the gut.
Urinating	Total drain of the bladder.
Vigilance behaviour (VB)	
Getting frightened	Short wince of the whole body.
Pausing	Freeze of motion with alert view and potential additional head lift and look about.
Laying down	Young boar presses its body abrupt even on the ground.
Guarding	Alert milling around, with lifted head and tail, obvious tense posture.
Foraging behaviour (FB)	
Pawing	Pawing in the ground (e.g. soil, leaves) with a foreleg.
Rooting	Rooting in the ground (e.g. soil, leaves) with the snout, also with brushing big branches aside.
Salt ingestion	Ingestion of salt at a salt lick by licking, nibbling.
Sucking attempt	Young boar attempt to suck on the sow's teats or briefly suck at the standing sow.
Suckling	Young boar are suckled by the lying sow.
Chewing	Uniform opening and closing of the mouth after foraging (feeding not visible).
Feeding attempt	Young boar takes soil/stone into its mouth.
Feeding	Ingestion of food with the mouth and chewing afterwards.
Drinking	Ingestion of water with the mouth.
Comfort behaviour (CB) – personal hygiene behaviour	
Stretching	Increasing the distance of the hind legs to the forelegs and slightly spreading of the hind legs while simultaneously scuttling with the forelegs.
Shaking	Moving its body strongly, briefly and fast back and forth while standing.
Rubbing	Rubbing one's body against a tree or another wild boar.
Nibbling	Nibbling/rubbing of the open mouth against the rubbing tree.
Scratching	Scratching one's body with the hind legs.

Scratching one's bottom	Rubbing one's bottom against the ground while sitting.
Rolling	Rubbing one's body against the ground.
Wallowing	Laying down (and optionally wallowing) in muddy water.

Social interaction (SI)

Active socio negative interaction

Threatening	Keeping another wild boar at distance by threatening behaviour.
Pushing away softly	Pushing another wild boar softly away with the head, the side of the body or the bottom.
Chasing away	A wild boar runs after another wild boar, which departs itself afterwards.
Snout knock	A wild boar knocks its head bottom-up in the direction of another wild boar (with/without touching).

Passive socio negative interaction

Retreating	A wild boar increases the distance to another wild boar, which emitted socio negative behaviour before.
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Socio positive interaction

Nose-to-nose contact	Sniffing at or touching the snout region (being sent of one or both wild boar, also at distance).
Nose-to-body contact	A wild boar sniffs at or touches another wild boar with the snout at its body or legs.
Playing	Playful behaviour against other wild boar (e.g. exercise fights, apparent copulation attempt).

Sexual behaviour (SB)

Copulation attempt	A wild boar climbs the bottom of another wild boar.
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Table 2 (on next page)

Results of the LMM and LSMEAN.

Comparison of the occurrence of each behavioural category with each other. The estimate and p-value of each pairwise comparison of means with Tukey adjustment is shown.

Table 2. Results of the LMM and LSMEAN. Comparison of the occurrence of each behavioural category with each other. The estimate and p-value of each pair wise comparison of means with Tukey adjustment is shown.

Pair wise comparison	Estimate	p-value
Locomotion – Olfactory behaviour	0,084	< 0,001 ***
Locomotion – Vigilance behaviour	0,106	< 0,001 ***
Locomotion – Foraging behaviour	0,120	< 0,001 ***
Locomotion – Comfort behaviour	0,141	< 0,001 ***
Locomotion – Social interaction	0,141	< 0,001 ***
Olfactory behaviour – Vigilance behaviour	0,023	> 0,05
Olfactory behaviour – Foraging behaviour	0,037	0,007 **
Olfactory behaviour – Comfort behaviour	0,057	< 0,001 ***
Olfactory behaviour – Social interaction	0,057	< 0,001 ***
Vigilance behaviour – Foraging behaviour	0,014	> 0,05
Vigilance behaviour – Comfort behaviour	0,034	0,014 *
Vigilance behaviour – Social interaction	0,035	0,012 *
Foraging behaviour – Comfort behaviour	0,020	> 0,05
Foraging behaviour – Social interaction	0,021	> 0,05
Comfort behaviour – Social interaction	< 0,001	> 0,05