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Wild boar space use and the determinants of its variation are crucial information for understanding wild boar *Sus scrofa* (L.) ecology and for wild boar management. Wild boar space use has mostly been investigated on broad temporal scales such as annual or seasonal home ranges. Ranges can vary depending on the observed timespan and on the temporal scales considered. The factors that affect space use variation can also depend on temporal scales.

In this study, we present an analysis of time series of daily ranging behaviour in wild boar. Using GPS-telemetry, we tracked 46 collared wild boars in southwest Germany. With the collected data, we calculated 6716 daily ranges of individuals based on at least 18 daily locations with near hourly location intervals. We compared three home range estimation methods and fitted multivariate models to assess the effects of the landscape, temporal and climatic factors or individual traits on the daily range size.

The daily range size varied significantly in the course of the year. The smallest daily ranges were covered from April to July, whereas the largest were covered in November and December. However, if the same days of the year are compared, lower temperatures reduced the size of daily ranges. Additionally, individual variation, social class, snow height, land use and elevation had a significant effect on the size of daily ranges.

Our results may be useful for planning protected areas, for monitoring wild boar populations, attributing agricultural damages to wild boar groups and for searching wounded or escaped animals. Moreover, the knowledge of daily used space may help to identify African swine fever (ASF) infection paths or design measures to reduce ASF risk including carcass removal, fencing projects or demarcation of management zones.

Keywords: African swine fever, home range, MCP, movement, space use, spatial behaviour

Wild boars *Sus scrofa* (L.) thrive under a wide range of environmental conditions (Podgórski et al. 2013) and the species is widely distributed around the world (Sjarmidi and Gerard 1988). The physical presence of wild boar is largely unnoticed by the public, because of their concealed lifestyle and mostly nocturnal activity (Keuling et al. 2008a, Brivio et al. 2017). Nevertheless, this large mammal influences ecosystems in many ways and is considered an ecosystem engineer (Barrios-Garcia and Ballari 2012, Genov et al. 2017).

In the last decades, wild boars have become a focus of wildlife managers, as their populations have increased in many parts of the world (Massei et al. 2015,

Bengsen et al. 2017, Pesendorfer et al. 2020). Climate change has led to fewer harsh winters and also favours boar foraging, for example, by causing more frequent tree mast years (Nussbaumer et al. 2018). Therefore, climate change is seen as a major driver in wild boar population development in Europe (Bieber and Ruf 2005, Melis et al. 2006, Massei et al. 2015, Vetter et al. 2015).

Human–wild boar conflicts are on the rise in spite of hunting (Frackowiak et al. 2013, Massei et al. 2015). Undesired economic effects arise due to wild boar activities such as their use of agricultural areas, private gardens and public greenspaces, accompanied by crop or property damage (Barrios-Garcia and Ballari 2012). Moreover, the function of wild boar as a vector of diseases and the current cases of African swine fever (ASF) in Europe and other parts of the world stress the importance of wild boar management. A spread of ASF into domestic pig farming causes severe economic losses (Gortázar et al. 2007, Meng et al. 2009,

De la Torre et al. 2015, European Commission 2018). Managing wild boar populations is considered a challenging task (European Food Safety Authority 2014). Detailed knowledge of the behavioural biology is needed for developing tailored wild boar management frameworks (Vicente et al. 2019). Therefore, a better understanding of factors which drive the spatio–temporal variation of wild boar behaviour is crucial (Nathan et al. 2008).

The area used by an animal during a specific timespan is of great interest to wildlife managers and ecologists as it is a key indicator for describing the relationship between an animal and its environment (Burt 1943). Moreover, wildlife ranges can easily be related to management units by comparing the respective areas. Wild boar home ranges have been estimated on different temporal scales (Keuling et al. 2008b, Podgórski et al. 2013, Jánoska et al. 2018). However, the factors which determine animal movement and the resulting range sizes are still not fully understood (Börger et al. 2008).

Space use is the result of many movement decisions which are determined by the interplay of individual traits, the internal state of an animal and the external environment (Börger et al. 2008, Nathan et al. 2008). There is already evidence for effects of numerous factors on movement of wild boar (Morelle et al. 2015). However, movement patterns of animals can be shaped by fine- and broad-scale movements, for example, daily patterns resulting from the locations of resting sites and feeding areas versus seasonal range shifts resulting from climatic factors and the emerging vegetation changes (Forester et al. 2007). The drivers of range size may vary on different temporal scales (Börger et al. 2006, Van Beest et al. 2011). Hence, for a comprehensive understanding of wild boar space-use patterns and the underlying causes, short-time scales must also be considered.

In our study we analysed daily used areas. The activity pattern of wild boar with mostly nocturnal activity and resting during daylight (Brivio et al. 2017) suggests that the cycle of 24 h is a biologically important period of wild boar behaviour. One day is also a relevant period in terms of wild boar management. We hypothesized 1) that the daily range size changes depending on the day of the year. Anthropogenic disturbances – particularly hunting – can trigger altered space use (Scillitani et al. 2010, Larson et al. 2016) and disturbance levels vary in the course of the year. Furthermore, ranges can be smaller if all life essentials – food, water, shelter, social partners – are available in proximity (Sanderson 1966). Changes in the availability of food and shelter may thus affect habitat quality and space-use patterns. A negative correlation of food availability and wild boar movement has been described by Singer et al. (1981) and Keuling et al. (2009). Temperate climate and varying daylight duration shapes time dependent vegetation and food availability at our study regions, with more scanty conditions during winter. Hence, we presumed 2) larger daily ranges during winter and 3) time dependent effects of the land-use type. At the same time, we expected 4) lower temperatures and 5) higher snow cover to be accompanied by smaller ranges because wild boars are less active (Brivio et al. 2017) and move less at low temperatures and with higher snow cover (Thurfjell et al. 2014). 6) For lower elevations we presumed smaller ranges, because a longer vegetation period at lower elevation may

offer better food supply. Furthermore, we hypothesised 7) a negative correlation of precipitation and daily range size as precipitation promotes greater likelihood of mud wallows at shorter distances and sodden soil facilitates rooting. It has been shown that wild boars are more active during brighter nights (Brivio et al. 2017); therefore, we assumed 8) that increased moonlight is accompanied by larger daily ranges. We also expected 9) a social class effect, with smaller ranges of females during the reproduction period (Janeau and Spitz 1984) and 10) significant differences between daily ranges of individuals.

Material and methods

Study region

We collared wild boars in three study regions in southwest Germany approximately 30–80 km north of Lake Constance: Swabian Alps (two collaring sites), Wurzach Marsh (two collaring sites) and Altdorf Forest (one collaring site; Fig. 1). Locations were recorded from April 2012 to December 2015. The study regions are situated in the natural-geographic regions Alpine Foreland and south-west German Low Mountain Range (Meynen and Schmithüsen 1960). West-wind dominated climate conditions with a mean annual temperature of 6–9°C and mean annual precipitation of 800–1000 mm shape the vegetation of the regions (Federal Agency for Nature Conservation 2018, University Hohenheim 2018). The coldest monthly mean air temperature at the wild boar sites was in February at −1.6°C whereas the warmest was in July at 18.5°C.

The majority of the landscape is used for agriculture or forestry (Table 1). Grain is usually harvested at the end of July to mid of August (Landwirtschaftliches Technologiezentrum Augustenberg 2018). The most common tree species are beech *Fagus silvatica* (L.) in deciduous broadleaf forest and European spruce *Picea abies* (L.) in conifer forests, respectively (Bundeswaldinventur 2012). In the study regions and during the observation period, European beech started to sprout leaves on average on 23 April and had lost half of their leaves on average on 31 October (DWD 2018b). Wolf *Canis lupus* (L.) was not present in the region and evidence for the presence of lynx *Lynx lynx* (L.) was found only very sporadically in the wider surrounding area. Roe deer *Capreolus capreolus* (L.) is the sole other wildlife ungulate occurring in proximity of the collaring sites (LAZBW 2017, MLR 2019).

Wild boar hunting is generally performed by foresters and licensed recreational hunters in state owned forests, and by recreational hunters on private and community properties. Common practices are solitary hunting from raised hides, many of which are placed near baiting stations (Keuling et al. 2008a), and occasional battues which usually take place in November or December. In the region, the largest monthly wild boar hunting bags were taken in November, December and January (Elliger 2015). As there was no closed hunting season for piglets during the study period, disturbances by hunting may have occurred all year.
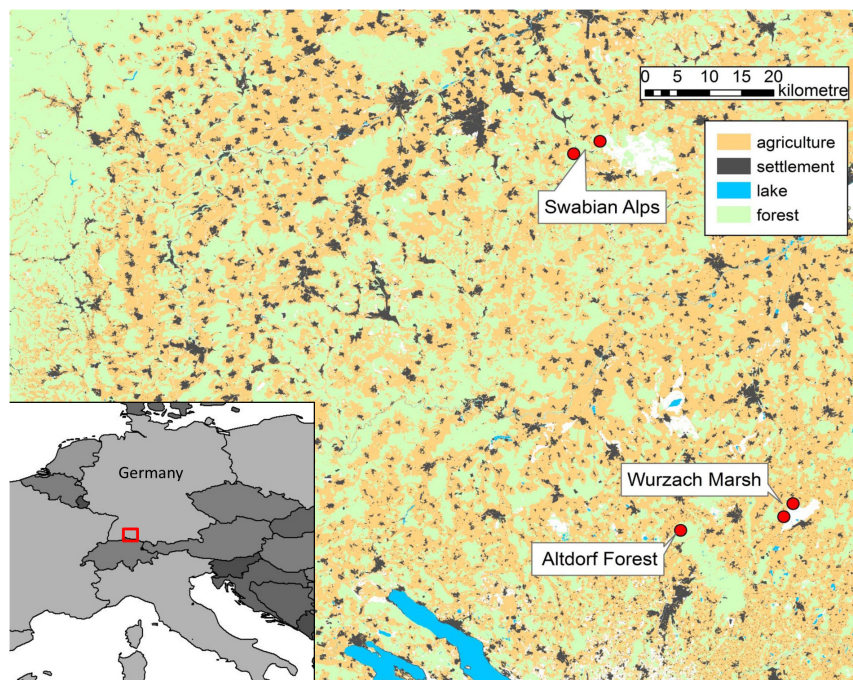
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Figure 1. Location of the collaring sites (red circles) and landscape mosaic (ATKIS 2015).

Data collection

We used maize as lure to capture wild boar in wood-clad corral traps with remote-controlled gates. The size of the traps was about 30 m². We drove the captured animals separately in a net tunnel, covered the eyes of the animals with mostly light-tight cloth and held the wild boar firmly with two or three persons while we fitted them with Vectronic Aerospace GPS Plus collars (Vectronic 2012). The collaring process took about five to ten minutes per animal and the wild boars were released thereafter at the collaring site. For welfare reasons, only animals heavier than 30 kg were collared. No animal died during capture and collaring. The collars were removed after an animal had been shot by a hunter during regular hunting or by a time controlled or remote triggered drop-off mechanism. The handling protocol was approved by the Ethics Committee of the Federal State Baden-Württemberg for Animal Welfare and fulfills their ethical requirements for research on animals (permit no. WFS1/12).

Age of the wild boars was recorded after visual assessment by experienced wildlife biologists at collaring based on size and coat colour. We applied this procedure because of animal welfare considerations (compare Fenati et al. 2008) as it allowed a faster processing of the captured animals in comparison to an age determination based on tooth eruption. The social classes were piglets, sub-adult (one to two years old animals) and adult. We assumed that the selected piglets were on average nine months old at the collaring event and reclassified them to sub-adult 90 days afterwards. Likewise, we assumed an average age of one and a half years for sub-adults and reclassified them to adult 180 days after collaring. Male and female piglets were pooled into one social class to accumulate a greater number of samples for this social class.

We removed locations recorded during the first 24 h after collaring to account for initial trapping and collar effects. We had analysed the movement behaviour of the wild boars during the first days after collaring by measuring the displacement of the wild boars from the traps. The used data did not show extraordinary displacements of the wild boars after the trapping event. Bauch (2015) observed that separately released animals met their sounder within less than 12 h. Many of the wild boars were captured as part of a sounder and thus subsequently were mostly roaming in groups. We considered individuals as walking alone during periods of at least one week that they spent away from their group. From sounders that were walking together, we included only one individual into the analysis, usually the heaviest female with the longest observation period and the highest position acquisition rate, for obtaining independent samples. Therefore, a sample animal may have walked alone, together with collard animals which were not included in the analysis or with animals not wearing a collar. We reduced the transmitted location data to samples with approximately one-hour intervals to diminish autocorrelation issues (Fieberg 2007). Data quality checks were performed in a PostgreSQL database (<www.postgresql.org/>) applying the procedure described by Urbano and Cagnacci (2014). For further data processing and statistical computing we used the software R (<www.r-project.org>).

Table 1. Land use in a 5 km buffer around the collaring sites (ATKIS 2015) and span of mean elevations of the daily locations.

Region	Land-use			Elevation (m)	
	Forest	Grassland	Cropland	min	max
Altdorf Forest	37.4%	30.6%	20.5%	477	783
Swabian Alps	30.7%	33.7%	17.1%	526	845
Wurzach Marsh	14.3%	41.5%	20.5%	600	756

Elevation and land-use category was extracted from a digital terrain model (ATKIS 2015). Agricultural land includes grassland and cropland. Hourly air temperature, daily precipitation and daily snow height were assigned to the locations based on the measurements at the nearest meteorological station (DWD 2018a). Air temperatures were elevation-corrected by $1°C \times 100^{-1} m^{-1}$. Furthermore, we computed a moon brightness index as the product of moon altitude above the horizon and moon illumination (Tischoff 2018) using the R-package 'suncalc' (Agafonkin and Thieurmel 2018), including moon altitude as radians and moon illumination ranging from zero (new moon) to one (full moon). Negative products were set to zero.

Data analysis

For space use estimation, we calculated minimum convex polygons including all locations (MCP100, Mohr 1947) and 95% minimum convex polygons (MCP95). Additionally, we applied a multiple convex hulls method for calculating 95% home ranges, using the single-linkage cluster analysis (LoHu95, Kenward et al. 2001). All areas were computed with algorithms of the R-package 'adehabitatHR' (Calenge 2006). We chose these methods, because they do not rely on parameter choices which may warp comparisons between our samples or hamper comparisons with other studies (Laver and Kelly 2008). For daily ranges, density based methods would lead to an underestimation of areas used during active behaviour because wild boar rest about half of the day (Brivio et al. 2017) and locations while resting are aggregated.

MCP100 is a strictly geometrical home range delineation with a long tradition (Odum and Kuenzler 1955), and is therefore frequently reported in space use studies (Russo et al. 1997, Keuling et al. 2008b, Laver and Kelly 2008, Podgórski et al. 2013, Jánoska et al. 2018). Although single displacements may lead to inflation of MCP100s, this is in line with our study objective, as we sought to quantify range dynamics on a daily basis and displacements may be a relevant part of wild boar behaviour. MCP100 is a reliable basis for assessing daily ranges for practical wild boar management because it describes a maximum area based on proven use.

In contrast to the all-encompassing MCP100, the applied algorithm LoHu95 measures a multinuclear range core by nearest neighbour cluster analysis and excludes the most excursive locations as well as areas between multiple delineated convex hulls. Whereas MCP95 excludes 5% of the locations which are furthest from the location centroid, LoHu95 excludes 5% of the locations based on the distance to the next locations (Kenward et al. 2001).

The reckonings of MCP100 and MCP95 were correlated at a Pearson coefficient of 0.98. Between MCP100 and LoHu95 the correlation was 0.70. Similarly, the logarithms ln(MCP100) and ln(MCP95) were correlated at 0.97, and between ln(MCP100) and ln(LoHu95) the correlation was 0.80. Because of the high correlation between the results of the different methods we state here mainly the results for MCP100 and report additional information concerning results based on the other methods in the Supplementary material Appendix 1.

We calculated the daily used areas for locations within the timespan from noon of a day until noon of the next day to take into account the mostly nocturnal activity of wild boar (Keuling et al. 2008a, Brivio et al. 2017). We did not exclude periods of displacement (e.g. juvenile dispersal, seasonal migration or responses to disturbances) and areas were only computed if a wild boar was located at least 18 times with near hourly intervals within the 24 h, to ensure that periods of activity are largely covered.

We assigned land-use category, air temperature, precipitation, snow height, elevation and moon-brightness to each wild boar location and its related time. As the locations of a noon-to-noon range were measured on two consecutive days the assigned values are based on the daily measurements on two days for snow height and for precipitation, however, based on hourly measurements for air temperature and precise to the second for moon brightness. Moreover, we transformed precipitation to ln(precipitation + 1) in order to improve the data distribution. As the next step we averaged the location-associated measurements of the variables over the locations of each daily noon-to-noon range or calculated proportions of locations per land-use category for this timespan. Finally, we assigned the day of the year attribute to each daily range.

For multivariate analysis we applied generalised additive models (GAMs, R-package 'mgcv') because they do not force linear relations between predictor and response but allow fitting smooth terms and thereby reveal effects of continuous predictors at a high level of detail (Wood 2011). The smooth terms for continuous predictors were fitted with the smoothing basis set to 'cs', while 'cc' was used for the cyclic predictor 'day of year'. Social class was included as parametric term. If both 'social class' and 'day of year' were considered in a model, social class was additionally included as an interaction smooth term 'day of year by social class' to allow a social class specific fitting of the day of year effect. Similarly, proportion of locations in forests and proportion of locations on agricultural land were included by the interaction terms 'proportion of locations in forests × day of year' and 'proportion of locations on agricultural land × day of year', respectively. With these interaction terms for land-use information and day of year we avoided to reflect only the patchy land-use mosaic of the landscape (small areas have more likely a high proportion of one land-use category). Because the mosaic of land-use categories is steady during the course of the year – with changing qualities within a category because of the vegetation cycle – the interaction term can reveal responses to time depended vegetation changes. Continuous predictors were mostly fitted by smooth terms with the initial setting k = 6, but k = 24 for day of year and k = (24,10) for interactions of day of year and proportion land-use type (Wood 2003). We checked the k-index using the 'mgcv' function 'gam.check' (Wood 2011).

The variability between individuals was accounted for by including wild boar identity (ID) as a random effect (bs = 're'). Moreover, the random effects 'study region', 'year' and 'number of locations per daily range' were included in all models. We controlled for temporal autocorrelation and included an autoregressive process of order 1 in the GAM. Because of the skewed distribution of the daily MCP100s, we transformed daily MCP100 to ln(daily MCP100) and

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Table 2. Daily MCP100 according to social class.

Social class	MCP100 (ha)					Date of maximum MCP100	Date of minimum MCP100
	Mean ± SD	Median	Density peak	Maximum	Minimum		
Adult males	69.6 ± 93.3	30.0	20.2	473.6	0.005	15 Sept.	16 Sept.
Adult females	53.8 ± 72.8	30.9	8.0	734.5	0.011	03 Dec.	04 Feb.
Sub-adult males	96.2 ± 182.4	47.7	19.3	4,542.2	0.070	20 Nov.	20 March
Sub-adult females	62.6 ± 93.6	33.8	10.1	1,599.8	0.004	27 Nov.	16 Dec.
Piglets	53.8 ± 72.9	29.3	12.8	816.9	0.014	18 June	12 Feb.

modelled ln(daily MCP100) as a Gaussian response variable. Daily MCP95s and daily LoHu95s were handled accordingly. Snow height and air temperature were correlated at a Pearson coefficient of −0.5; all other predictors showed weaker correlations.

We excluded data of adult males and piglets from the models for analysing only social classes in which at least three wild boar individuals were represented in each month of the year. Model performance was controlled using the R function 'diagnostics' (van Rij et al. 2017). For comparing models and effect sizes we calculated Akaike information criterion (AIC) and adjusted R^2-values (R^2adj) based on maximum likelihood models (Richards et al. 2011).

Sample size

With each area estimation method we calculated 6716 daily ranges. Of these, 779 represent areas used by piglets, 1632 areas used by sub-adult females, 2134 areas used by sub-adult males, 2034 areas used by adult females and 137 used by adult males. The underlying locations originate from 46 wild boars, some of which changed social classes during the observation period. The daily home ranges are based on locations of 15 piglets, 20 sub-adult females, 16 sub-adult males, 17 adult females and 2 adult males.

The GAMs are based on 5800 daily ranges of 43 individuals, omitting observations of piglets and adult males. On average, 134.9 ± SD 123.7 daily ranges were computed per individual. The mean number of locations is 23.7 ± 1.85 locations per daily range.

Results

Altogether, the daily MCP100 areas are characterised by a mean of 69.7 ± 124.3 ha (Supplementary material Appendix 1 Table A1, for MCP95 and LoHu95). Piglets and adult females had the smallest mean MCP100s. For all social classes, the medians of daily MCP100 areas remain below 48 ha (Table 2). The density distribution of the daily MCP100 areas has a pointed peak for all classes (Fig. 2).

The data show mean daily ranges often below 50 ha during April, but larger daily mean areas during fall and winter (Fig. 3).

When comparing GAMs, the predictor 'proportion of locations on agricultural land' improved the AIC the most (Table 3, model M5), followed by 'day of year' and 'proportion of locations in forest'. We used the full model M1, which had the lowest AIC, for further investigation. The estimated size and direction of partial effects of model M1 are shown in Fig. 4–9; we report the model coefficients in the Supplementary material Appendix 1 Table A2.

Model M1 reveals, in accordance with hypothesis 1 (H1), variation of the daily ranges during the year (Fig. 4) and larger daily ranges during winter than during summer (H2) for all social classes. Almost throughout the entire year, sub-adult males covered the largest daily ranges. Their daily ranges decreased steadily from December to July and increased during autumn, until they reached a peak in December. The estimates for the female classes depict an increase in area at the end of February and first half of March followed by a steep decline in March and April. After June, both sub-adult and adult females had predominantly increasing ranges until November and December, respectively. In November, the areas of sub-adult females were larger compared to the ranges of adult females; in December this relation was reversed. The estimates of the different methods MCP100 (Fig. 4), MCP95 (Supplementary material Appendix 1 Fig. A3) and LoHu95 (Supplementary material Appendix 1 Fig. A4) showed similar temporal dynamics on different range size levels, with more steady LoHu95 predictions in comparison to both MCP predictions.

The data of the tracked wild boars did not indicate daily ranges with great proportions of locations on agricultural lands from mid-March to mid-May or in November. The estimates for daily ranges depending on DoY and proportion of land use type supported H3. In our prediction scenario, daily ranges with a great proportion of locations on agricultural lands were smaller from December to February than during summer. In contrast, daily ranges with a
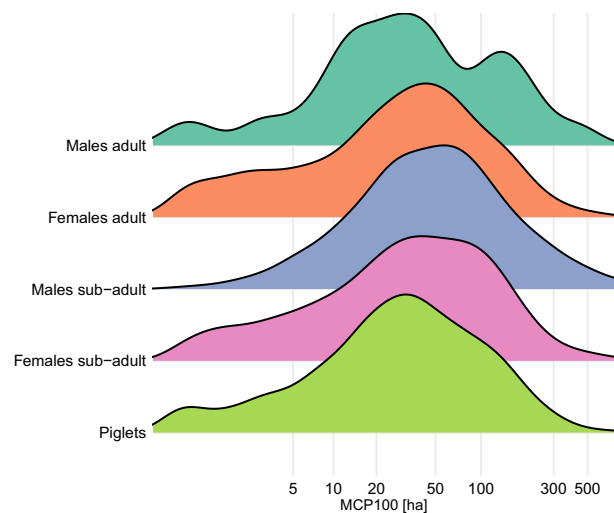

Figure 2. Density distribution of daily MCP100 areas by social class; x-axis is on ln-scale; density of areas exceeding 600 ha not shown; consider the low sample size for adult males.
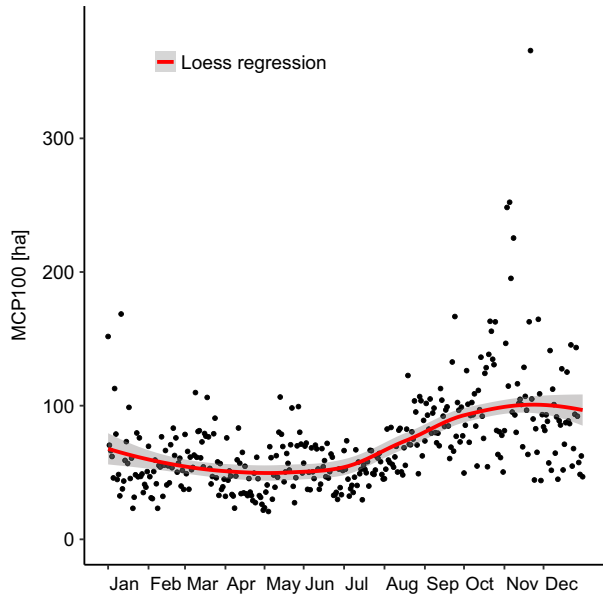
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Figure 3. Mean daily MCP100 for each day of the year; $N_{MCP100} = 6716$; 365 daily averages over wild boar individuals of all social classes and a Loess smoother with span = 0.8; confidence interval = 0.95.

proportion of approximately 0.2 locations on agricultural lands were larger during winter than during summer (Fig. 5).

Daily ranges with proportions of locations in forest (Fig. 6) above 0.7 differed in size during the course of the year between approximately 10 ha and 40 ha. For daily ranges with proportions of locations in forest between 0.1 and 0.5 the variation was greater. With such proportions, a daily range size of approximately 20 ha was predicted during summer, however more than 110 ha in December and January. Small daily ranges of fewer than 14 ha were predicted for April combined with proportions of locations in forest above 0.8.

Lower mean air temperatures led to smaller daily home ranges, consistent with H4. Our additive model considers the effects of daily mean temperature and day of year separately. An exemplary summarization of the two effects is depicted in Fig. 7 which illustrates the variation of daily range sizes in the course of the year at varying temperatures for the same day.

Increasing snow height reduced daily ranges significantly ($p < 0.05$, Fig. 8A), as expected (H5). Elevation also had a significant effect on daily ranges. Higher elevations were mostly paralleled by larger daily ranges, however both ends of the span of elevation values were accompanied by smaller daily ranges (Fig. 8B). In contrast to our expectations (H7 and H8), precipitation and moon brightness had no significant impact (Supplementary material Appendix 1 Table A2, Fig. A5). The data supported H10 and revealed pronounced variation of daily ranges both between individuals and within individuals (Fig. 9). The SD of the intercepts of the random effect ID was 0.5.

Discussion

Our data show a significant variation of daily ranges in the course of the year (supporting H1), and different temporal

Table 3. GAMs for predicting daily MCP100, sorted by AIC (best first); the random effects wild boar ID, year, region and number of locations are included in all models; shaded terms are included in the model; NA = term not included.

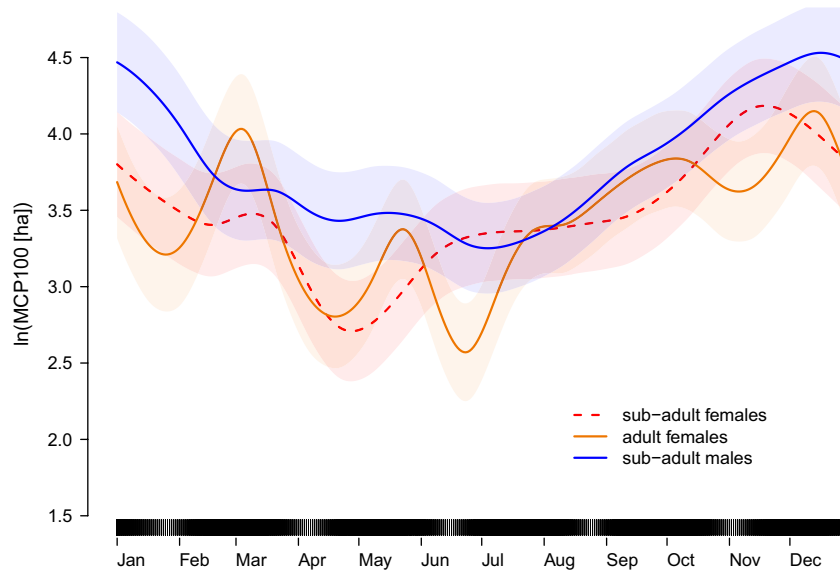| Model	Social class	Day of year	Proportion forest	Proportion agriculture	Temperature	Precipitation	Snow height	Elevation	Moon brightness	R²adj	AIC	ΔAIC to M1
M1										0.40	18543.8	–
M7						NA				0.40	18544.5	0.7
M9									NA	0.40	18544.5	0.7
M6					NA					0.40	18553.6	9.8
M8							NA			0.40	18563.9	20.1
M2	NA									0.39	18589.2	45.4
M10								NA		0.39	18650.3	106.5
M4			NA							0.37	18765.9	222.1
M3		NA								0.33	18888.3	344.5
M5				NA						0.34	18938.1	394.3

Figure 4. Estimated daily range ln(MCP100 [ha]) depending on day of the year and social class; other continuous predictors set to the median: proportion forest = 0.8, proportion agriculture = 0.1, daily mean air temperature = 10.2°C, elevation = 657 m, ln(precipitation + 1 [mm]) = 0.4, snow height = 0 mm, moon brightness = 0.02, random effects cancelled; consider also Fig. 5–9 for additional effects; model M1; reference degrees of freedom for DoY-splines = 22; shades indicate one standard error; data of piglets and adult males were omitted in the models because of low sample size.

patterns between the social classes (supporting H9). Pronounced differences of daily range sizes also exist between individuals (supporting H10). The predictor day of year and the interaction of day of year with the proportion of locations on agricultural land or in forest had the strongest effect on the size of daily ranges when comparing models (supporting H3). Moreover, the daily space use was modulated by air temperature, snow height and elevation (supporting H4, H5 and H6).

The average daily MCP100 area of 69.7 ha amounts to 1.4% of the average annual home range of 4845 ha which we estimated for wild boar in the study region (Johann et al. 2019).

Russo et al. (1997) reported a mean daily MCP100 area of 33 ha for wild boars observed during spring and summer in an Italian no-hunting zone. Podgórski et al. (2013) analysed the effect of urban habitat versus primeval forest on daily ranges in Poland (mean 240 ha and 130 ha) and Jánoska et al. (2018) described daily used areas in Romanian lowlands versus high hills (mean 94.2 ha and 119.4 ha). Some studies reported variation of seasonal wild boar ranges based on seasonal classification of boar locations (Boitani et al. 1994, Calenge et al. 2002, Santos et al. 2004, Keuling et al. 2008b). Our multivariate analysis confirms seasonal variation and shows for the first time the day-to-day variation of
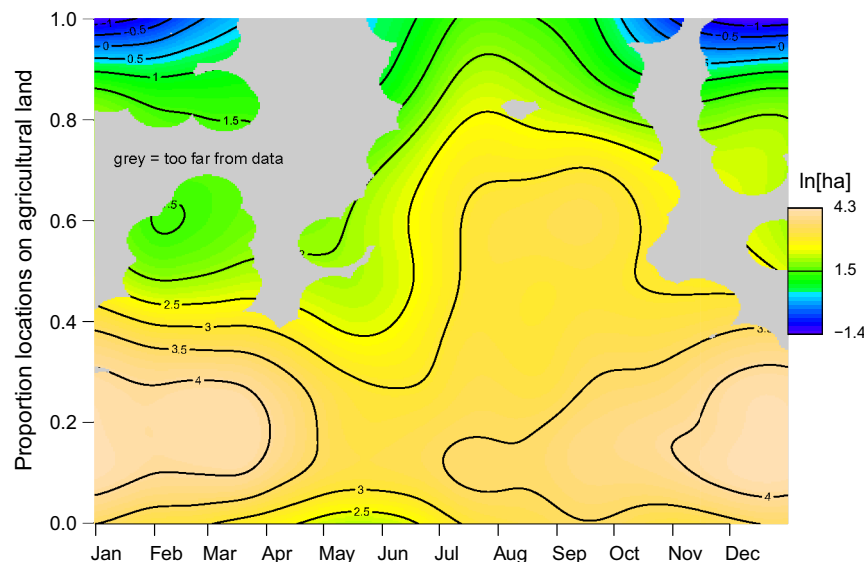

Figure 5. Estimated daily ln(MCP100) depending on the additive effects interactions proportion locations on agricultural lands and day of year; proportion locations in forest set to 0, other continuous predictors set to the median: daily mean air temperature = 10.2°C, elevation = 657 m, ln(precipitation + 1 [mm]) = 0.4, snow height = 0 mm, moon brightness = 0.02, social class = sub-adult males, random effects cancelled; model M1; consider also Fig. 4 and Fig. 6–9 for additional effects.
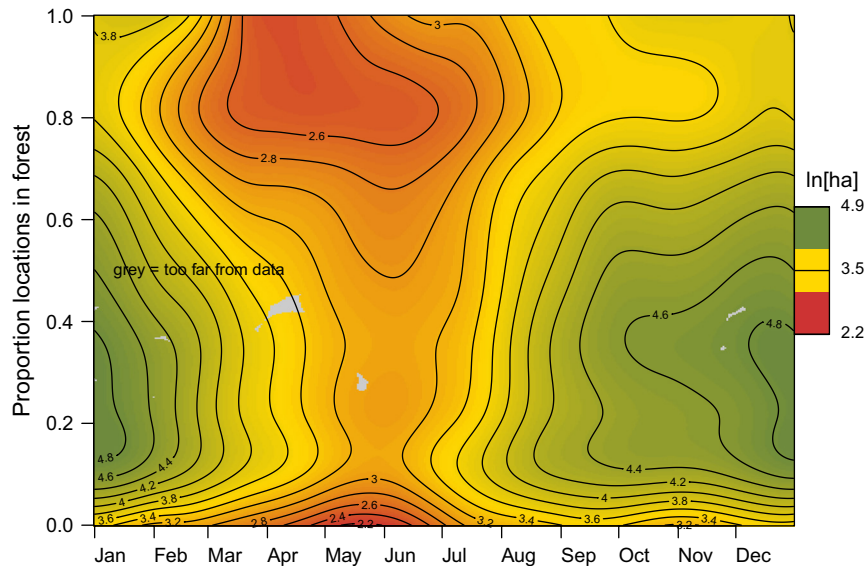
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Figure 6. Estimated daily ln(MCP100) depending on the additive effects interactions proportion locations in forest and day of year; proportion locations on agricultural land set to 0, other continuous predictors set to the median: daily mean air temperature = 10.2°C, elevation = 657 m, ln(precipitation + 1 [mm]) = 0.4, snow height = 0 mm, moon brightness = 0.02, social class = sub-adult males, random effects cancelled; model M1; consider also Fig. 4, 5 and 7–9 for additional effects.

space use in the course of the year along gradients of additional isolated factors. Our findings suggest that wild boars adapt daily space use strongly in accordance with their social class and actual local conditions.

Ranges can be smaller if all resources are available in proximity. This concept has been shown as applicable for different species (Simon 1975, Larter and Gates 1994, van Beest et al. 2011). The day of the year curves (Fig. 4) support H2 by showing that daily ranges are smaller in spring and early summer. Food and cover are more abundant during the vegetation period. In July, most field crops are approaching maximum height and provide optimal cover.

In early autumn, the daily ranges predominantly increase. Harvested fields may force boars to adopt longer wanderings for staying close to cover at the forest edge or to shift their ranges into the forests for finding food and cover. Tree mast is the preferred diet of wild boar (Schley and Roper 2003). Andrzejewski and Jezierski (1978) observed particularly high food intake during the last quarter of the year. Building up fat reserves favours overwinter survival (Vetter et al. 2015). Increased food demand and distances between mast trees may have contributed to larger daily ranges in autumn. Moreover, after leaves fall, wild boar may have to travel longer distances between feeding- and well covered resting-sites.
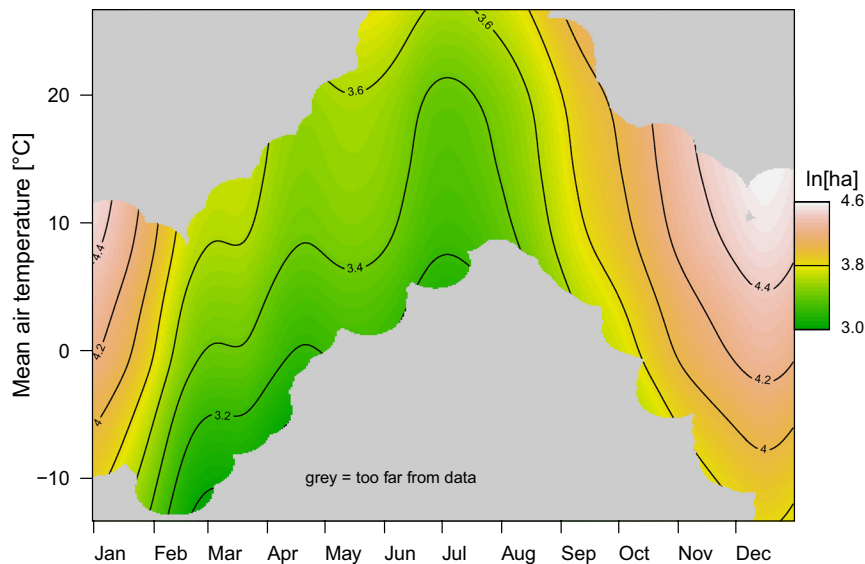

Figure 7. Estimated daily ln(MCP100) depending on day of the year and daily mean air temperature; other continuous predictors set to the median: proportion forest = 0.8, proportion agriculture = 0.1, elevation = 657 m, ln(precipitation + 1 [mm]) = 0.4, snow height = 0 mm, moon brightness = 0.02; model M1, social class set to sub-adult males; random effects cancelled; consider also Fig. 4–6, 8 and 9 for additional effects.
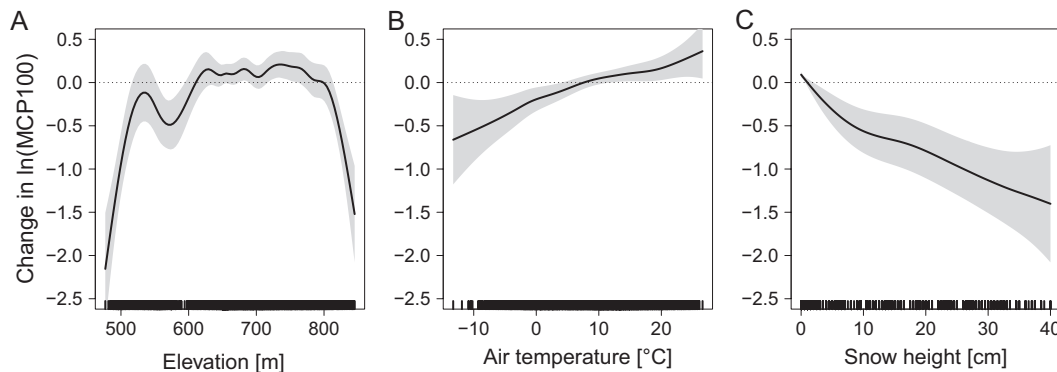
Figure 8. Partial effects of snow height (A), elevation (B) and air temperature (C) on ln(MCP100); shades indicate one standard error; the dotted lines indicate the mean of the fitted values; model M1; consider also Fig. 4–7 and 9 for additional effects.

Wild boar hunting from hides at bait stations is a common practice in Germany (Keuling et al. 2008a). Access to artificial food resources, especially during the winter, may affect ranges (Boitani et al. 1994). We identified several bait stations in the study regions by visualising GPS-locations and received confirmations for the bait sites by the hunters in charge. The provided food probably has contributed to the observed range decrease in December and January in the female classes.

Peaks of daily ranges are predicted for November and early December. Hunting events have been identified in several regions as a factor which triggers movement (Maillard and Fournier 1995, Calenge et al. 2002, Sodeikat and Pohlmeyer 2003, Tolon et al. 2009, Scillitani et al. 2010) and thus increases daily wild boar ranges. November to January is the main hunting period in the study region and flight reactions of collared wild boars to hunting and

hunting preparation have been observed (Bauch 2015, 2017). These events may have contributed to larger ranges in November and December.

Our data confirm significant differences between individuals (supporting H10) and show different small scale temporal patterns of range variation between social classes. However, the parametric term 'social class' did not have a significant effect in M1, which may be influenced by the additionally included interaction term 'day of year by social class'. Female wild boars separate and use small areas around parturition (Janeau and Spitz 1984). The lows of daily ranges of females in mid-April and end of April in our data suggest that the females gave birth to their young mainly during this period. Increasing movement potential of their offspring may have caused increasing ranges of the female wild boars after these lows. The area increase for females before the reproduction period may be due to the search for a nest site
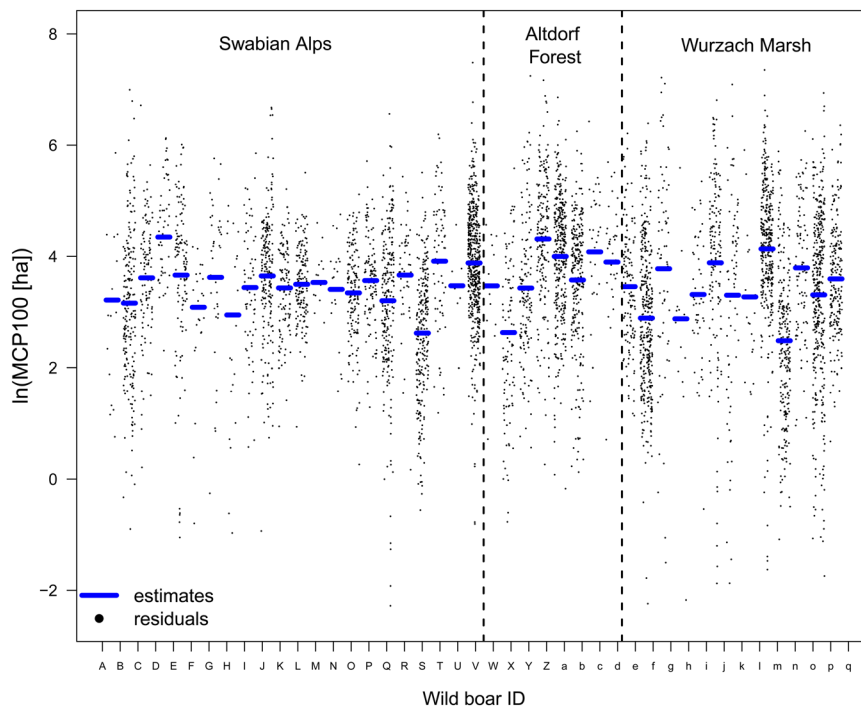

Figure 9. Estimated daily ln(MCP100) per ID and partial residuals. Other predictors set to the median or most common category; model M1; consider also Fig. 4–8 for additional effects; see Supplementary material Appendix 1 Table A3 for social classes of the represented wild boars.

(Gundlach 1968). The smallest daily ranges in April were accompanied by proportions of forest above 0.8 (Fig. 6), which suggests that forest is a preferred vegetation type during the reproduction period.

Some studies depict larger seasonal range sizes for males in winter–spring compared to females (Kurz and Marchinton 1972, Singer et al. 1981, Boitani et al. 1994). In terms of daily ranges, Russo et al. (1997) reported significant differences between male and female wild boars. Sexual behaviour of male wild boar has been suggested as a driver of this variability (Boitani et al. 1994). Our results show increasing daily ranges during autumn for all social classes. However, the area increment between end of July and end of December was the largest in sub-adult males. This suggests that dispersal of sub-dominant males increased during rutting time in late autumn (Briedermann 2009). Dispersal increases daily ranges not only because of the distance travelled to another region, but also because the animal cannot benefit from known feeding grounds or resting sites and must explore the landscape (Andreassen et al. 2002).

Keuling et al. (2010) reported a wild boar dispersal proportion of 15.4% in north Germany. The large daily ranges during winter at proportions of locations in forests from 0.2 to 0.6 may also reflect displacement behaviour in which wild boars used both forests and open land. Proportions of locations on agricultural lands above 0.9 during winter were accompanied by very small daily ranges. This may show the use of small areas which offer cover with landscape elements such as hedgerows, copses or fallow vegetation.

Mammals cope with environmental temperature fluctuations through a wide range of behavioural strategies (Terrien et al. 2011). Our data show a significant effect of mean air temperature on daily range size (supporting H4). Ranges were larger in winter. However, lower mean air temperature at the same day of year led to smaller ranges. This is in accordance with the findings of Brivio et al. (2017), who observed less wild boar activity at low daily maximum air temperature and Thurfjell et al. (2014), who reported decreased movement at low winter temperatures. Similarly, Singer et al. (1981) described a wild boar preference of sunny slopes for day beds and restricted movement on cold winter days. Frost and snow hamper rooting and access to food (Welander 2000) and a change of locality is complicated by snow cover (Sweeney and Sweeney 1984). Basking, resting in contact and reduction of movement reduces metabolic costs at cold temperatures and may be the energetically best option (Signer et al. 2011, Arnold et al. 2015, Gallagher et al. 2017). Harsh weather also may have discouraged hunters and thus may have limited disturbance by hunting resulting in smaller daily ranges. The larger daily ranges at very high temperatures during summer could be caused by greater distances from foraging to cool resting sites or to places for wallowing. If climate change brings milder winters and hotter summers, wild boar will probably respond with larger daily ranges.

The effect of the predictor elevation with mostly larger ranges at higher elevations lends some support to the view that a longer vegetation period reduced daily ranges of wild boars (supporting H6). The small daily ranges at both ends of the span of elevation values (Fig. 8) probably reflect just the fact that extreme high or extreme low daily average values are more likely if the animals don't use large areas which include different elevations, together with the given low sample size at the ends of the elevation values.

H7 and H8 were not underpinned by the analysis. Precipitation had no significant effect on daily range size at the given temperate climate and from the all-the-year viewpoint of the used predictor term. Moon brightness index also had no significant impact, which may be influenced by the fact that we did not consider the cloudiness (Supplementary material Appendix 1 Table A2; compare Brivio et al. 2017).

Conclusions

Our data showed significant changes of daily ranges in wild boar in the course of the year. This variability emphasises the relevance of stating the time of the year at which locations have been measured when reporting wild boar home ranges.

The variable 'day of year' was a proxy for time-dependent changes of external and internal drivers of daily range sizes, some of which may be unknown. Moreover, the timing of the main hunting season (November and December) coincides with activity during mating season and changes in food availability by the onset of winter. Disentangling the relative importance of these factors requires further research.

Our findings emphasise the relevance of considering the time of the year, land use, air temperature and snow cover when assessing daily space use. Our results may be useful for planning protected areas, landscape design, monitoring, searching for escaped or wounded animals and for assigning agricultural damages to wild boar groups. In terms of the function of wild boars as vector of diseases, knowledge of areas used by healthy animals provides relevant benchmarks to answer the question of where an infected animal found dead had been in its last days of life. This may help efforts for disease control such as identifying ASF infection paths or demarcation of management zones (compare Lange et al. 2018, Mysterud and Rolandsen 2018, Morelle et al. 2019).

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Supplementary material (available online as Appendix wlb-00609 at <www.wildlifebiology.org/appendix/wlb-00609>). Appendix 1.