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Authors: Lemel, Jonas, Truvé, Johan, and Söderberg, Bo

Source: Wildlife Biology, 9(s1) : 29-36

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/wlb.2003.061

Variation in ranging and activity behaviour of European wild boar *Sus scrofa* in Sweden

Jonas Lemel, Johan Truvé & Bo Söderberg

Lemel, J., Truvé, J. & Söderberg, B. 2003: Variation in ranging and activity behaviour of European wild boar *Sus scrofa* in Sweden. - Wildl. Biol. 9 (Suppl. 1): 29-36.

The present wild boar *Sus scrofa* population in Sweden mainly originates from animals that have escaped from enclosures. At some locations wild boars have evidently been released deliberately. Whatever their origin, rapid increases in both number and distribution of free-ranging wild boars have occurred. As wild boars are considered exotic in the Swedish fauna, sportsmen very often provide supplemental food in varying degrees, partly to facilitate and secure hunting possibilities, partly to keep wild boars out of farmed crops. In this paper we describe wild boar activity behaviour and intend to show how wild boar adjust their activity behaviour under different ambient conditions. The aim of our study was to increase the knowledge of managers to improve hunting effectivity and risk assessment concerning crop damage. The wild boars were, almost without exceptions, active during night. The mean time for an activity bout was 7.2 hours and the wild boars in the study area were only to a minor degree adjusting their activity bout to the prevailing night length. However, the hour of sunset seemed to be the cue which triggered the onset of activity bouts. The mean distance that the wild boars travelled during activity bouts was 7.2 km and the estimated mean activity range was 104.4 ha. The mean effort when roaming the activity range was 110.9 m/ha. A substantial variance was typical for all activity variables. For activity distance, 72% of the variation was explained by adding wind speed, season, minimum temperature and snow cover to our model. Significant effects of minimum temperature, snow cover and an interaction between activity time and minimum temperature explained 42% of the variation in activity range. The variation in relative air humidity explained 41% of the time active during an activity bout.

Key words: activity adjustment, ranging and activity behaviour, Sus scrofa, Sweden, wild boar

Jonas Lemel & Bo Söderberg, Swedish Association for Hunting and Wildlife Management, Öster Malma, SE-611 91, Nyköping, Sweden - e-mail: jonas.lemel @telia.com (Jonas Lemel)
Johan Truvé, Department of Applied Environmental Science, Box 464, SE-405 30, Göteborg University, Sweden - e-mail: johan.truve@miljo.gu.se

Corresponding author: Jonas Lemel

The wild boar *Sus scrofa* is an omnivorous mammal (Briedemann 1990) typically ranging in border zones between forests and pastures used for agricultural production (Dardaillon 1986, 1987, Gerard, Cargnelutti, Spitz, Valet & Sardin 1991, 1992) and showing only slight temporal differences in behaviour between the sexes (Massei, Genov, Staines & Gorman 1997). The reintroduction of wild boars into Sweden has caused much debate, as its foraging behaviour occasionally causes damage to farmed crops (Briedemann 1990). As tenancy in Sweden normally does not include hunting rights, and as wildlife managing responsibility solely is with those who have the legal right to hunt, the effect of free-ranging wild boars calls for effective management.

In a management perspective, it is important to describe the ranging patterns and the factors influencing activity bouts in order to confine at which scales area management should be carried out. Wild boar appear to be highly mobile (Singer, Otto, Tipton & Hable1981, Spitz & Janeau 1990) and this will have two apparent consequences: 1) the risk of having crops damaged may not be confined to the neighbourhood of the area in which a group of wild boars locate their resting sites, and 2) the risk of overestimating the number of wild boars is imminent as a single group of wild boars may be taken as different animals and thereby be counted twice or more.

In general, little information is published on how the animals react to seasonal changes (but see Labudzki & Wlazełko 1991) and how prevailing weather conditions affect their activity (but see Cresswell & Hareris 1988, Bright, Morris & Wiles 1996, Bronikowski & Altmann 1996). Most of the published literature concern the effect of density-independent factors on population levels (Lewellen & Vessey 1998, Loison & Langvatn 1998, Pontier, Festa-Bianchet, Gaillard, Jorgenson & Yoccoz 1998).

In this paper, we intend to describe the variation in ranging and activity as well as in parameters which convey information about wild boar activity, such as ranging distance, activity time, activity range and effort on an annual basis for free-ranging wild boar in Sweden. We will correlate ambient factors such as air temperature, wind speed, relative humidity and snow coverage to the activity variables in an attempt to explain the observed variations in the variables. The wild boar is an almost exclusively nocturnal animal, and as the European wild boar has a south-northernly distribution ranging from northern Africa to the border of the northern coniferous zone (Briedemann 1990), the difference in latitudinal distribution cause wild boars to experience different variations in the length of night. In the south, the number of dark hours varies within 8-12 hours whereas in the north, summer nights are short and winter nights long. Therefore, wild boar in the northen distribution zone should be expected to adjust their foraging and other activities according to the northern night regime. During winter, wild boars in our study area might be expected to extend their activity time whereas the opposite might be the case during summer. Supplemental feeding is common in our study area, partly as a means to reduce the risk and/or the magnitude of damage to crops, partly to facilitate hunting by attracting wild boars to sites where fodder is provided.

Material and methods

We conducted the field work at two locations in mid-east Sweden (Björkvik 16° 32' 9.6", 58° 50' 9.6" and Stavsjö 16° 25' 48", 58° 43' 12") where the coniferous forest of Kolmården borders farming pastures southwest of Lake Yngaren. The habitat gradually changes from pure forest stands of spruce *Picea abies* and pine *Pinus sylvestris* into large open cropping fields. In-between, fields and meadows are forming a mosaic structure with the forest. Our study was based on telemetric positioning of 28 radio-tagged wild boars of different sex and age. Tagged wild boars were located by radio cross-positioning and sighted by eye as far as possible every 20 minutes simultaneously by two persons. Each tracking session began before the animals left their resting locations and was carried out until the wild boars were back at their resting places. Sometimes the animals changed their resting position and went to a new location at the end of an activity bout. At such occasions, the tracking was stopped when no movements were recorded. The time, position on the UTM-system and bearing was recorded every 20 minutes, or, if an animal was 'lost', new bearings were taken as fast as possible. Contact between the trackers was made after each telemetric bearing by means of walkie talkies or mobile telephones to check audibility and angle of intersection. After a radio location was taken, the position was approximately recorded on a map (1:20,000) to optimise the intersection angle of the bearings after the relocation of trackers. The majority (23) of the wild boars was tagged with ear-radio senders of the types THX-1 or THX-2 (Televilt International AB) and the remaining five caught animals were tagged with neck collars of the type MOD500 (Telonics). We strived to perform activity tracking once a week, and when possible more than one animal was tracked. Incomplete and unrealistic activity bouts were dismissed from the data set. Each radio location was calculated using the SAS programme for two bearing estimations of location (White & Garrot 1990). All sessions were processed using SAS for Windows, version 6.10 or 6.11 (Statistical Analysis System, Cary, NC, USA). Radio locations were excluded if error polygons exceeded 2 ha (i.e. if the probability is 90.25% that a location is within the error polygon of a maximum size of 20,000 m^2). The mean error polygon for the data set is 650 ± 158 m^2 (SD; minimum = 0 m^2, maximum = 18,650 m^2; N = 2,065). Due to the road net in the field area, a bearing was rarely taken more than 500 metres from the position of an animal. The audibility distance of the weakest transmitter (THX-1) was up to 1,400 m. Rapid movements, however, sometimes generated distances of more than 500 m and affected the quality of the radio location. Distances between radio locations were calculated by:

$$\text{distance}_i = \sqrt{(\text{x-location}_{i+1} - \text{x-location}_i)^2 + (\text{y-location}_{i+1} - \text{y-location}_i)^2}$$

If animals were sighted by eye, locations were recorded on a map (1:20,000), and their coordinates were added to the data set with the error polygon set to zero.

All sets of telemetric observations were analysed for any effect of ambience factors. During the study, data on minimum temperature, relative air humidity, wind speed and snow cover were collected every 24 hours in the study area. The temperature factor was divided into three levels: < -5°C, -5°C-5°C and > 5°C. Relative air humidity was factorised into three levels: dry(< 50%), intermediate (50-75%) and moist (> 75%). The wind speed factor was also divided into three levels: calm weather (< 1m/second), low wind speed (1-2 m/second) and strong winds (≥ 3 m/second). The factor containing snow cover was divided into two levels: no snow and ground covered by snow. As an additional factor, the year was subdivided into three periods: April-July, August-October and November-March. This subdivision is justified, as the three periods have different assets for the wild boar. In April-July, the natural production of food sources in the study area is most pronounced. In August-October, the access to ripening and ripe wheat and oats, which are the most important varieties of cereals in the study area, is at its maximum. November-March is characterised by typical winter conditions with no or very low natural production of food sources.

All analyses were carried out using GLIM 4.0 (NAG, British Statistical Society) where the minimum adequate model for each variable was calculated (Crawley 1993). Variables were log-transformed if they deviated significantly from the normal distribution.

Results

Activity, movements and ranging

The activity time was normally distributed (W = 0.971, P < W = 0.2486) with a mean of 7.2 ± 0.169 hours (S.E.; N = 77; Fig. 1A). The range was 7.84 hours and the span between the first and third quartile was 1.84 hours.

The total distance travelled during an activity session departed significantly from a normal distribution (W = 0.947, P < W = 0.0038) and had a mean of 7.2 ± 0.352 km (S.E.; N = 85; Fig. 1B). The median distance travelled (6.1 km) departed only slightly from the arithmetic mean, and the span was 3.7 km between the first and third quartile (Q_1 = 5.0 km, Q_3 = 8.7 km). The distribution of transport distance within 20-minute time spans, however, deviated drastically from normality (W = 0.669, P < W = 0.0001). The arithmetic mean (0 = 301.1 ± 386.8 m (SD; N = 1,573) departed from the

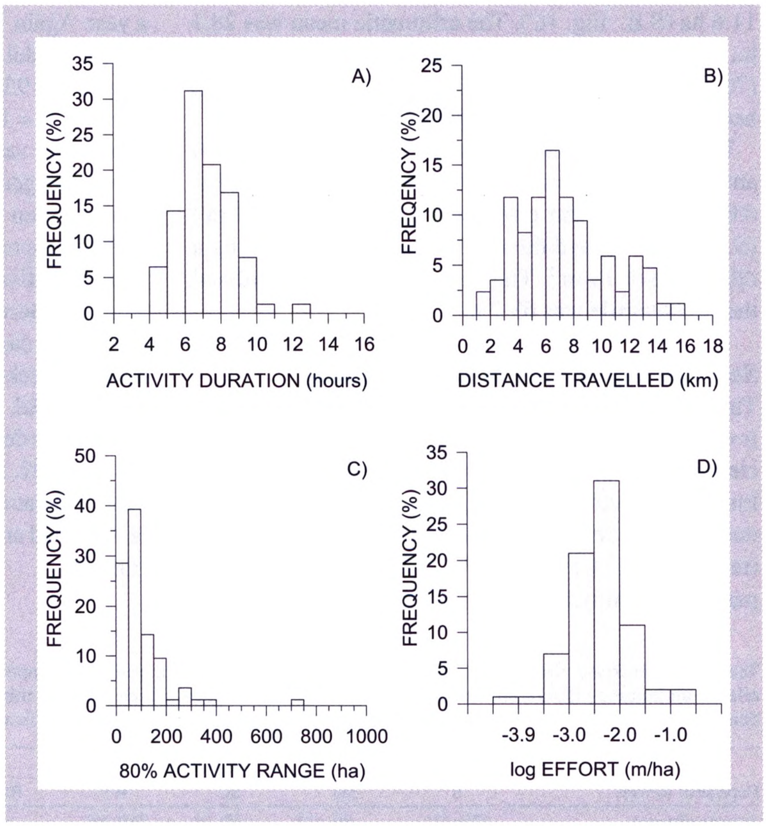

Figure 1. Frequency (in %) distribution of duration of wild boar activity bouts (A), distance travelled during activity bouts (B), 80%-activity range during activity bouts (C) and effort spent during activity (D).

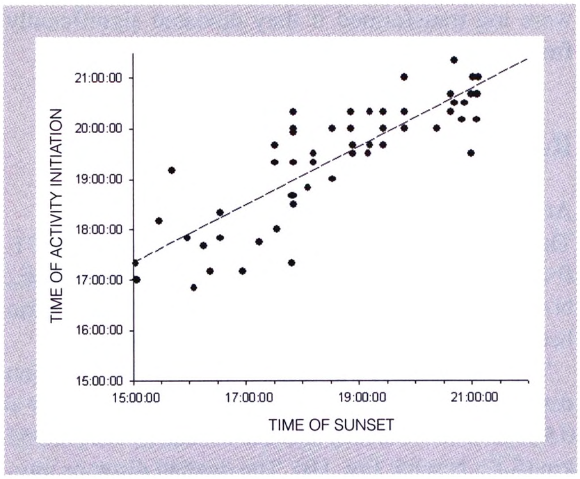

Figure 2. Correlation between time of sunset and intiation of wild boar activity bouts (r = 0.87).

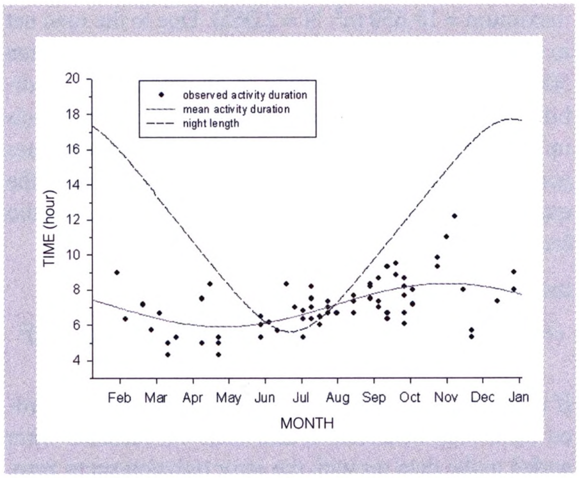

Figure 3. Duration of wild boar activity bouts (in hours) related to time of year and seasonal change in length of night in the study area.

median (169.7 m) with 131.4 m, and the difference between the third and first quartile was 295.6 m.

The wild boar 80%-activity range also deviated from a normal distribution (W = 0.704, P < W = 0.0001), and the arithmetic mean for the activity range was 104.4 ± 11.6 ha (S.E.; Fig. 1C). The arithmetic mean was 28.1 ha larger than the median size of the activity range (76.3 ha). The range was 709.9 ha and the difference between the third and first quartile was 81.8 ha.

The effort a wild boar spent per ha was low (Fig. 1D) and departed from normality (W = 0.702, P < W = 0.0001). The mean effort was 110.9 ± 0.00968 m^{-1} (S.E.; N = 76), and the median was 91.9 m^{-1} giving a difference of 19 m^{-1}. The range between the third and the first quartile was 63.2 m^{-1}.

Seasonal dependence of activity timing

Timing of activity initiation was strongly correlated (r = 0.87) with the hour of sunset (Fig. 2), and the association was best described by a quadratic polynomial: Initiation of activity = $b_0 + b_1 \times \text{week} + b_2 \times \text{week}^2$. The deviance was reduced by 98.63 from 119.06 to 20.424 (residual df = 74, $r^2 = 0.83$, F = 178.69, P ≤ 0.0001). All parameter estimates of the polynomial significantly deviated from zero (b_0 = 15.49 ± 0.2912, t = 53.19, P ≤ 0.001; b_1 = 0.3748 ± 0.02161, t = 17.34, P ≤ 0.001; b_2 = -0.006987 ± 0.0003750, t = 18.63, P ≤ 0.001). A similar pattern appeared for termination of activity, indicating that the time used for activity was relatively constant over a year. Again, a quadratic polynomial was a minimal adequate model explaining the pattern. However, the deviance of 195.07 was reduced by only 94.70 (residual df = 74, $r^2 = 0.48$, F = 35.122, P ≤ 0.0001), leaving a substantial variance unexplained. The fit revealed that wild boars generally ended activity sessions well before sunrise, even when nights are long, and that the activity time appears relatively constant over a year. If the time of activity is constant, no correlation between week and duration of activity should be expected. This was not the case. Instead, there was a positive relationship between week and duration of activity. The minimal adequate model, however, was a cubic polynomial that reduced the deviance from 169.09 to 144.4 (residual df = 74, $r^2 = 0.32$, F = 11.619, P ≤ 0.0001). This fit showed that the duration of activity was at a minimum at the end of April and at a maximum in the beginning of November (Fig. 3).

Table 1. Summarised effects of the six explanatory factors season (S), minimum temperature (MT), snow cover (SC), wind speed (WS), relative air humidity (RAH) and the interaction effect between activity time (AT) and minimum temperature (MT) on four different dependent variables describing activity bouts of Swedish wild boars. ns indicates non-significance; * = P ≤ 0.05, ** = P ≤ 0.01, *** = P ≤ 0.001.

	Explanatory factors						Model statistics	
Dependent variable	S	MT	SC	WS	RAH	AT*MT	r^2	Pr > F
Activity distance	12% ***	9% ***	3% **	76% ***	ns	ns	0.72	0
Activity area, 80%-range	ns	50% ***	12% **	ns	ns	38% ***	0.42	0
Activity effort, 80%-range	ns	62% *	38% *	ns	ns	ns	0.13	0.017
Activity duration	ns	ns	12% *	18% **	70% ***	ns	0.41	0

Table 2. Effect of the three explanatory factors wind speed, relative air humidity and snow cover on the duration of an activity bout (estimates in hours). ns indicates non-significance; * = P ≤ 0.05, ** = P ≤ 0.01, *** = P ≤ 0.001.

Factor	Level	Estimate		Effect
Wind speed	calm weather	0.2	ns	levels intercept
	1 - 2 m/second	0.98	*	increased duration
	> 3 m/second	6.3	intercept	
Relative air humidity	<50%	-2.37	**	reduced duration
	50 - 75%	-1.53	***	reduced duration
	>75%	6.3	intercept	
Snow cover	no snow	1.31	***	increased duration
	snow	6.3	intercept	

Table 3. Effect of the four explanatory factors wind speed, season, minimum temperature and snow cover on the log-transformed distance travelled during an activity bout (estimates in hours). ns indicates non-significance; * = P ≤ 0.05, ** = P ≤ 0.01, *** = P ≤ 0.001.

Factor	Level	Estimate		Effect
Wind speed	calm weather	-0.67	***	reduced distance
	1 - 2 m/second	-0.16	ns	
	> 3 m/second	1.98	intercept	
Season	November-March	-0.10	ns	
	April-July	-0.32	***	reduced distance
	August-October	1.98	intercept	
Minimum temperature	< -5°	0.39	***	increased distance
	-5° - 5°	0.00	ns	
	> 5°	1.98	intercept	
Snow cover	no snow	0.55	***	increased distance
	snow	1.98	intercept	

Factors affecting activity time, distance, area and effort

A considerable unexplained variation remained in activity time, suggesting that additional factors influence the duration of an activity bout (Table 1). The total distance of roaming during an activity bout together with the mean velocity and the 80%-activity range explained a substantial part of the residual variation (activity duration = 2.05 + 5.84 × log (distance) - 5.16 × velocity - 0.39 × log (activity range; $r^2 = 0.64$, $F_{(3, 73)} = 43.16$; $P_{b0} \leq 0.0007$, $P_{b1} \leq 0.0001$, $P_{b2} \leq 0.0001$, $P_{b3} \leq 0.0516$), rejecting the effort × ha^{-1} as a non-significant term. By adding factorised meteorological terms to the model, only a slight increase in the degree of explanation was observed (r^2: 0.64 → 0.70). This implied that the effect of meteorological factors was nested within distance, velocity and activity range.

Among the meteorological factors, wind speed, relative air humidity and snow cover appeared to have significant influence on activity duration (Table 2). When wind speed was low (1-2 m/second), the wild boars significantly extended their activity bout with almost one hour, and this contrasts their behaviour in weather conditions with either stronger winds or calm weather (see Table 2). When the ground was covered by snow, the wild boars reduced their activity bout with approximately one and a half hour (see Table 2). The largest effect, however, was caused by the relative humidity of the air. In dry air conditions, the wild boars significantly reduced their activity time with roughly two and a half hour, and in intermediate humidity conditions, the time spent on foraging and other activities significantly decreased by two hours (see Table 2).

The distance travelled during an activity bout was also influenced by prevailing weather conditions, and the effect of wind speed explained a substantial part of the residual variance (see Table 1). Compared to calm weather conditions, the wild boars were significantly more disposed to increase the distance travelled throughout an activity bout when more windy conditions prevailed (Table 3). There were also significant seasonal influences. The wild boars reduced the distance travelled during a bout from April to June (see Table 3). Low temperatures (< -5°C) caused the wild boars to significantly increase the distance passed during the activity (see Table 3). Furthermore, the wild boars reduced the activity distance significantly when the ground was covered by snow (see Table 3).

Also, the area of activity was affected by environmental factors (see Table 1). Most important was the prevailing temperature. When the minimum temperature was < -5°C and when the ground was covered by snow, the wild boars significantly increased their activity range (Table 4). There was also a significant interaction effect between minimum temperature and activity time. The rate of increase in activity range was positively and significantly correlated with activity time both when in-

Table 4. Effect of the three explanatory factors minimum temperature, snow cover and the interactions between minimum temperature and activity duration on log 80%-activity range. (estimates in hours) ns indicates non-significance; * = P ≤ 0.05, ** = P ≤ 0.01, *** = P ≤ 0.001.

Factor	Level	Estimate		Effect
Minimum temperature	< -5°	4.02	***	increased range
	-5° - 5°	-0.58	ns	
	> 5°	1.75	intercept	
Snow cover	no snow	1.17	***	increased range
	snow	1.75	intercept	
Minimum temperature × Activity time	< -5°	-0.18	ns	
	-5° - 5°	0.3	***	increased range with time
	> 5°	0.19	*	increased range with time

Table 5. Effect of the two explanatory factors minimum temperature and snow cover on log effort during an activity bout (estimates in hours). ns indicates non-significance; * = P ≤ 0.05, ** = P ≤ 0.01, *** = P ≤ 0.001.

Factor	Level	Estimate		Effect
Minimum temperature	< -5°	-0.55	**	reduced effort
	-5° - 5°	0.01	ns	
	> 5°	-1.79	intercept	
Snow cover	no snow	-0.64	***	reduced effort
	snow	-1.79	intercept	

termediate and higher temperature regimes prevailed. In colder weather conditions (≤ -5°C), the activity range tended to be reduced by increased activity time (see Table 4).

Finally, the activity effort was influenced by both snow cover and minimum temperature (see Table 1). When minimum temperatures dropped below -5°C and when the ground was free from snow, the wild boars significantly reduced their activity effort (Table 5).

Discussion

The observation that wild boar activity time does not oscillate with the same amplitude as night length does over a year at the latitude of the study area may, in opposition to a study on badgers *Meles meles* (Cresswell & Hareris 1988), seem to be caused by access to food. It is likely that wild boars in our study area would be forced to spend more hours active to fulfill their energy requirement, especially during winter time, if no supplemental food was provided. The nocturnal life, however, appears not be obligate. When wild boars are not threatened by hunting or other human activities, activity during day-light hours has been reported (SOU 1980). Also, according to the staff at the Natural Park at Coto Doñana, Spain, the residing wild boars in the Doñana Park need to be active 24 hours in order to meet their energy and nutrition needs, as food access is scarce. Cuartas & Braza (1990) report that the wild boars in Coto Doñana (Spain) allocated 60% of their activity to foraging.

The wild boars in our study area ate supplemental food provided by local sportsmen who supplied it to reduce the risk of damage on farmed crops and to facilitate hunting. It is obvious that supplemental feeding influenced the time that the wild boars in our study area needed for foraging. Nevertheless, the mean time active is not constant over a year, and a substantial variance in activity remains to be explained. In our study, the wild boars, almost without exceptions, did not change resting sites during day-light hours (i.e. the wild boars were found in the evening at the site where they ended an activity bout). This implies that any activities during day-light hours took place in the immediate vicinity of the resting site (Spitz & Janeau 1990).

Apparently, the wild boars in our study adjusted the onset of an activity bout quite well to the hour before sunset. The activity onset, however, appeared to be delayed about two hours after sunset.

The time active was observed to be at its minimum (approximately six hours) in April-May, and this does not coincide with the fact that the number of dark hours is at its minimum in June. This may be ascribed to the fact that a substantial part of the sow population is constrained by the mobility of their piglets (Singer et al. 1981). Another aspect which may influence the activity time is the accessibility of natural food, in as far as the ground frost has broken up and the production of natural food items has increased. Furthermore, the activity bouts reached their maximum earlier than should be expected (October-November) solely based on the ambient light regime. This may be caused by the fact that wild boars in our study area built up fat deposits in order to meet the lowered accessibility to food in the coming winter.

Even if the variables are correlated, a substantial part of the residual variance could be explained at a level of significance by adding factors such as wind speed, relative air humidity, ambient minimum temperature, snow cover and season. As experiments that actually test dependencies are lacking, this part of the discussion should merely be viewed as speculations that may encourage further studies on activity budgets for wild boars.

According to our results, the time the wild boars in the study area spent active depended on wind speed, relative air humidity and whether or not the ground was covered by snow. The significant increase in activity (almost one hour longer) at conditions with weak winds compared to circumstances with calm or more windy conditions, may depend on optimal conditions for the wild boars to catch the scent of humans, sporting dogs or other potential dangers. Of course, it is possible that such conditions promote the possibilities for the wild boars to find resources, such as carcasses, as well. This interpretation fits equally well to the observation that wild boars in our study area adjusted their activity time to the relative air humidity. When drier and intermediate conditions prevailed, the wild boars reduced their time of activity by two and a half hours and two hours, respectively, compared to the activity time in humid conditions. For hunters, it is common knowledge that sporting dogs pick up scents more easily when the ground is moist. This might also be true for wild boars, as the wild boars in the study area became more active in humid conditions which should optimise the possibilities of finding a food resource. In addition, the correlation between relative air humidity and activity time may as well reflect a security aspect (Twigg, Lowe, Gray, Martin, Wheeler & Barker1998).

The observation that wild boars in the study area reduced their activity time with almost one hour when the ground was covered by snow may solely be a result of wild boars being more keen to visit sites where supplemental food was provided. The distances that the wild boars travelled during an activity bout, ranging from 1 km to 16 km, were apparently very variable. Concerning the prevailing wind speed, the wild boars seemed only to adjust their behaviour when there was no wind by reducing the distances travelled. Again, this may be related to a reduction in their possibilities of detecting a danger as any scent will be transported very slowly in situations with no wind. According to our field observations, the wild boars seemed to be very cautious before they entered a feeding site; thus they took a route around the site prior to entering it as if they were checking for scents in all directions.

We also found a seasonal effect, in as far as the distance travelled was reduced during April-July. It is likely that the abundance of suitable food resources is not critical at this time of the year and hence, the wild boars were less forced to undertake longer foraging journeys. When the ambient minimum temperature dropped below -5°C and the ground was covered by snow, the distance travelled increased. As these conditions occur during the winter season, it is tempting to speculate that wild boars are more prone to check more feeding sites during the foraging bout at this time of the year.

The area covered during activity bouts ranged within 3.6 - 713.5 ha and was affected by minimum temperature, snow cover and an interaction effect between minimum temperature and activity time. The activity area increased when the minimum temperature dropped below -5°C and the ground was covered by snow. It is tempting to suggest that the wild boars visited more feeding sites as they were more in need to fulfill their energy requirements. The interaction effect between minimum temperature and activity time shows that the wild boars in the study area adjusted their foraging behaviour by keeping the activity area smaller at higher temperatures. This suggests that wild boars are more restricted by the energy budget when temperatures are low. Finally, the effort the wild boars spent when active appeared to be reduced when the prevailing temperature dropped below -5°C and increased when the ground was covered by snow. Likewise, these results suggest that the costs in terms of energy consumption of roaming about become higher when the weather is cold. The reason for an increased effort when the ground was covered by snow, may be related to wild boars being more prone to visit sites where food was supplied.

Management implication

Our study shows that wild boars are highly mobile and that a group of wild boars under certain conditions will visit several sites at which supplemental food is provided. This implies that groups of sows and their piglets, under some conditions, roam on more than one hunting ground during an activity bout. If judgement of the population size is based on uncoordinated counts, the risk of over-estimation is evident. This risk could be reduced if counts are coordinated to be undertaken on the same date and at the same time, and if the number of and times for observations are checked afterwards.

Concerning the question on what impact the mobility and activity of wild boar groups have on crop damage, it is evident that wild boars can travel distances covering several hunting grounds during an activity bout. Even if a site, where supplemental food is provided, and a site where wild boars have their resting sites are located seemingly far away from cropping fields, this will offer no guarantee that damage will not occur to farm land. This fact calls for cooperation between several hunting teams if hunting should be used as a means to both regulate the population and reduce damage on farmed crops.

Acknowledgements - we thank the Research fund of the Swedish Association for Hunting and Wildlife Management, the Swedish Environmental Protection Agency and Karl Erik Önnersjös foundation for scientific research for financial support. We also thank Karl-Henry Lundin, Conny Pettersson, Caesar and Elisabeth Åfors and Leif Fredriksson for necessary and valuble assistance. The study was performed by permission of the Swedish Environmental Protection Agency (permissions 94-DNR-360-46655-94 NF and 98-DNR-413-828-98-NV) and The Uppsala Ethical Committee of Animal Experiments (permissions C275/94 and C47/98).

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