

Spatiotemporal behavioral plasticity of wild boar (*Sus scrofa*) under contrasting conditions of human pressure: primeval forest and metropolitan area

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The aim of this study was to examine the effects of sex and age of individuals, season, and human pressure (both human presence and habitat structure) on spatiotemporal behavior of wild boar (*Sus scrofa*). Specifically, we compared wild boar behavior under contrasting conditions of human pressure, within the primeval temperate forest of Białowieża (eastern Poland) and the metropolitan area of Cracow (Poland). It was predicted that, compared with the forest, wild boar within the urban area will have smaller home ranges due to restricted space, will show longer daily movements due to patchy resources, and will exhibit increased nocturnal activity and ranging behavior in an attempt to avoid human interference. We used radiotracking data from 35 wild boar. Animals inhabiting the urban area had smaller home ranges, yet covered almost twice as much distance on a daily basis than individuals inhabiting primeval forest. Daily duration of activity was similar in the 2 study areas. However, distribution of activity throughout the day differed considerably. In the urban area wild boar were almost exclusively nocturnal, whereas in the primeval forest wild boar activity was evenly distributed throughout the day. Additionally, in the urban area, activity was strongly associated with traveling speed, whereas in the primeval forest active wild boar moved about to little extent. Seasonal effects were stronger in the primeval forest and affected daily distance traveled, duration of activity, and level of diurnality. This study showed that wild boar can adjust their spatiotemporal behavior to local conditions and this may be one factor explaining recent rapid demographic expansion in Europe.

Key words: activity, daily distance, home range, Poland, space use, urban area

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DOI: 10.1644/12-MAMM-A-038.1

The ranging behavior and spatiotemporal activity of mammals reflect interactions between individuals and their environment. Numerous factors have been shown to affect home range size: body size, sex, and age (McLoughlin and Ferguson 2000; McNab 1963; Mysterud et al. 2001), food abundance and distribution (Clutton-Brock and Harvey 1978; Taitt 1981), population density and social structure (Damuth 1981; Jetz et al. 2004), and risk of predation (Tufto et al. 1996). However, the importance of each factor depends on the scale of analysis, i.e., species, population, or individual level (McLoughlin and Ferguson 2000). Similarly, observed patterns of temporal activity are shaped by intrinsic and extrinsic factors. Internally controlled activity rhythms are influenced by a number of cyclic environmental factors, such as photoperiod, temperature fluctuations, regular feeding bouts (Daan and

Aschoff 1982), and temporal disturbances (e.g. predation, human interference—Keuling et al. 2008a; Kitchen et al. 2000).

In addition to these factors that, often interactively, shape spatiotemporal behavior of mammals, human activity modifies behavior and home ranges of animals. Human pressure (e.g., hunting, tourism) can directly affect behavior and may result in shifts toward nocturnal activity (Kitchen et al. 2000) or influence movements and space use patterns (Frank and Woodroffe 2001; Jeppesen 1987). In contrast, human activity may indirectly influence behavior because human-induced



habitat fragmentation has a profound effect on the spatial behavior of mammals due to the creation of patchy resource distribution and barriers that constrain animal movements (Campbell-Smith et al. 2011; Tolon et al. 2009; Vistnes et al. 2004).

Studies have highlighted considerable intraspecific variation in home range size of wild boar (*Sus scrofa*), but with no clear pattern with regard to sex and age-related differences, seasonal changes, and geographic location (Baber and Coblenz 1986; Boitani et al. 1994; Keuling et al. 2008b; Lemel et al. 2003; Massei et al. 1997; Russo et al. 1997; Singer et al. 1981). In mammals, it is predicted that changes in home range size are inversely related to population density (“density-dependent hypothesis”—Abramsky and Tracy 1980; Wood and Brenne-man 1980) and food availability (“food-exploitation hypothesis”—Larter and Gates 1994). However, studies testing these hypotheses in wild boar populations reached conflicting conclusions (Bertolotto 2010; Massei et al. 1997).

Besides considerable variation in spatial behavior, temporal patterns can also be modified by several factors. Wild boars are active for approximately 12 h a day and their activity is mainly confined to dusk, dawn, and night (Boitani et al. 1994; Keuling et al. 2008a; Lemel et al. 2003; Massei et al. 1997; Russo et al. 1997; Singer et al. 1981). The duration and distribution of activity is affected by weather conditions (Lemel et al. 2003), habitat type (Boitani et al. 1994; Singer et al. 1981), and seasonality (daylight length, food availability; Keuling et al. 2008a). However, these studies were conducted in areas with high levels of human interference (e.g., hunting) and/or areas transformed by human activities, which may alter the natural behavior of the species. Information on wild boar ranging behavior and activity in undisturbed ecosystems is lacking.

In response to human activities, wild boar can adjust their spatiotemporal activity in an attempt to avoid human contact or to take advantage of the human-induced changes within the landscape. For example, wild boars have been shown to increase their nocturnal activity in response to increased hunting pressure and in proximity to human settlements (Keuling et al. 2008a). Furthermore, hunting pressure affects home range size (Maillard and Fournier 1995; Sodeikat and Pohlmeier 2001) and can cause temporary range shifts to ensure access to seasonal food resources offered by agricultural crops (Keuling et al. 2009).

In recent decades the wild boar numbers within Europe have increased significantly (Apollonio et al. 2010; Sáez-Royuela and Telleria 1986). This creates potential for serious conflicts between humans and wild boar in agricultural regions as well as densely populated rural and urban areas (Geisser and Reyer 2004). Several factors have been proposed that may have contributed to increase of wild boar densities, such as increasing global temperatures, more frequent mast fruiting events, as well as management practices that are ineffective in regulating population numbers (Bieber and Ruf 2005). However, the expansion of populations and their growth may be partially attributed to the behavioral plasticity of the species.

In this paper, we compared the activity and spatiotemporal behavior of wild boar populations in 2 contrasting environments differing in human pressure, namely one population inhabiting the primeval temperate forest of Białowieża (eastern Poland) and another inhabiting the metropolitan area of Cracow, the second largest city in Poland. These 2 areas differ in human pressure (both human presence and habitat structure), with high exposure in Cracow and low in primeval forest. This study is the first direct comparison between populations to investigate wild boar behavioral plasticity under contrasting conditions of human pressure and habitat structure. We hypothesized that, compared with primeval forest, wild boar within urban areas will have smaller home range sizes due to restricted space; show increased daily movement due to patchy resources; and exhibit increased nocturnal activity and ranging behavior to avoid human interference.

MATERIALS AND METHODS

Study area.—The study was conducted in 2 areas of Poland—Białowieża Primeval Forest in the eastern part of the country and a metropolitan area of Cracow in the south—characterized by profound differences in human pressure and habitat structure (Fig. 1). The Białowieża Primeval Forest (BPF)—located on the Polish–Belarusian border (52°47′N, 23°48′E; ~1,450 km²)—is the last remnant of the European temperate lowland forest. Within Poland, BPF (600 km²) is dominated by 3 main forest types, including a high proportion of old growth: pedunculate oak (*Quercus robur*), small-leaved lime (*Tilia cordata*), European hornbeam (*Carpinus betulus*) stands, mixed coniferous stands, and European ash (*Fraxinus excelsior*), black alder (*Alnus glutinosa*) stands.

The study area was located in the center of the Polish part of the BPF. The study area consisted of 92.6% forest, 7.2% open land (meadows, river valleys), and 0.2% anthropogenic areas (e.g., allotments)—Corine Land Cover database (European Environment Agency, <http://www.eea.europa.eu/>). Two-thirds of the study area was within the borders of the Białowieża National Park and its buffer zone, where hunting is prohibited, motorized traffic is allowed only under permission from the National Park, and forest managements are limited to sanitary cutting and fencing off regeneration areas. Tourists are restricted to day hikes on designated trails and overnight camping is prohibited. The remaining part of the study area is within the commercial part of the BPF, where limited logging and hunting occur. However, hunting from fixed locations is only permitted at a few designated sites. Motorized traffic in the commercial part of the BPF is allowed only for forestry service vehicles. Human density in the Polish part of the BPF is about 7 inhabitants/km² and the density of roads accessible for 2-wheel-drive is about 1.2 km/km² in the commercial part of the forest (Theuerkauf et al. 2003). However, there was no human settlement in the close vicinity of the study area.

The density of the wild boar population is estimated to be 2.35 ind./km². In addition to wild boar, four other ungulate species occur in the forest, including red deer (*Cervus elaphus*),

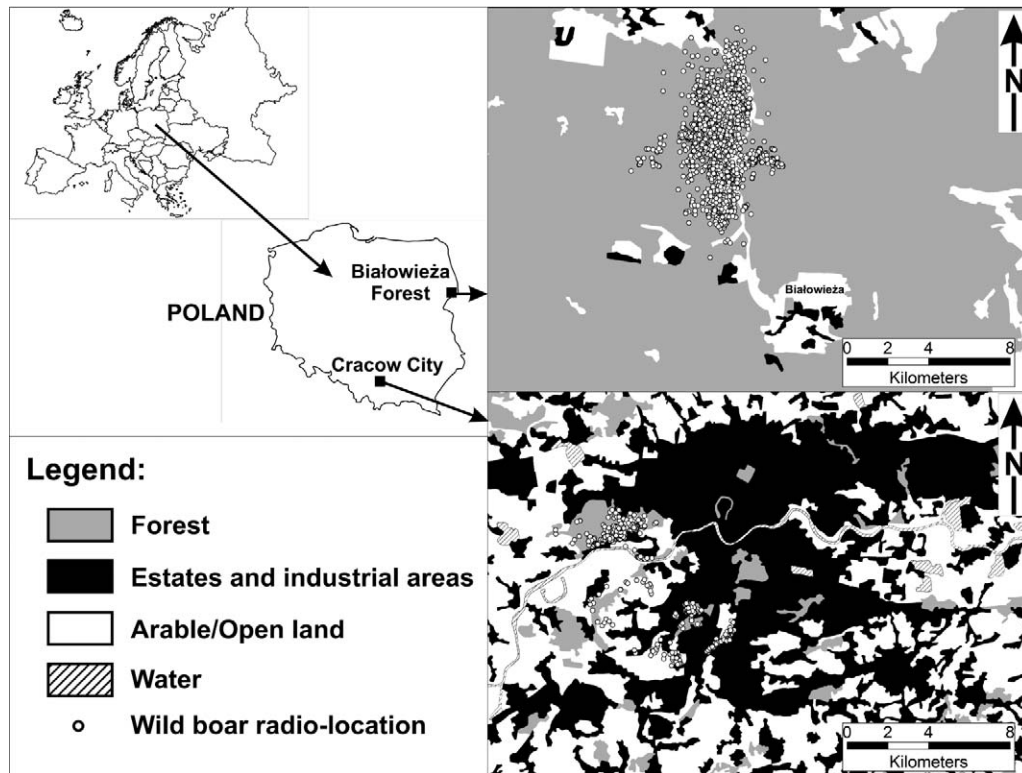


Fig 1.—Maps detailing location of the study areas in Poland and radiolocations of wild boars (*Sus scrofa*; all individuals) in the study areas. In Cracow City, areas occupied by radiotracked wild boar consisted of 18% forest, 43% arable/open land, and 39% estates and industrial areas, whereas in Białowieża Primeval Forest 92.6%, 7.2%, and 0.2%, respectively.

roe deer (*Capreolus capreolus*), moose (*Alces alces*), and the European bison (*Bison bonasus*). Two large carnivores, Eurasian lynx (*Lynx lynx*) and wolf (*Canis lupus*), also occur in stable populations (Jędrzejewska and Jędrzejewski 1998). The climate is transitional between Atlantic and continental types, with stronger influence of the latter (Jędrzejewska and Jędrzejewski 1998). Mean January temperature is -4.1°C and the mean number of days with snow cover is 105 (Institute of Soil Science and Plant Cultivation, <http://www.zazi.iung.pulawy.pl/>). Annual precipitation ranges from 550 to 600 mm (Institute of Geography and Spatial Planning, Polish Academy of Sciences, <http://www.igipz.pan.pl/>).

The second study area, Cracow metropolitan area, is located in the south of Poland ($50^{\circ}1'N$, $19^{\circ}53'E$). Cracow is the second biggest city of the country, with an estimated human population of 750,000. Approximately one-third of the city area is covered with meadows, pastures, orchards, arable lands, parks, and woods. The wild boar population in this area is located in the peripheral part of the city and its habitat is a mosaic of woods, parks, open land (meadows, gardens, and agricultural fields), and anthropogenic areas (housing estates, warehouses, and industrial estates). Forests, covering 4% of the city, are mainly concentrated to the western part and largely consist of European beech (*Fagus sylvatica*) and pedunculate oak-dominated stands. Radiolocations were taken over a 40-km² area in the western part of the city and consisted of 18% forest, 43% open land, and 39% anthropogenic area (Corine

Land Cover database). Roe deer is the only other ungulate sympatric species within the city limits. Single-hunter hunts are permitted in the outskirts of the city and nearly one-half of the wild boar population is harvested annually. Wild boar population density is estimated to be 0.15 ind./km² within this area (unpublished data of the Institute for Nature Conservation, Polish Academy of Sciences, Cracow). Mean January temperature is -2.1°C and the mean number of days with snow cover is 62. Annual precipitation ranges from 650 to 700 mm (Institute of Climatology, Jagiellonian University, Cracow, <http://www.klimat.geo.uj.edu.pl/>).

Trapping and radiotracking.—Data were collected between February 2006 and December 2008. The same method was used to capture wild boar in both study areas: cage and wooden traps ($1.5 \times 1 \times 2$ m) and large drop-net traps (Jędrzejewski and Kamler 2004) baited with maize. A combination of Zoletil (tiletamine and zolazepam) and Domitor (medetomidine) mixture (1:0.025 ratio) was administered intramuscularly to immobilize captured wild boar. Atipemazole hydrochloride (Antisedan) was used as an antidote (Kreeger 1997). In some instances a combination of ketamine and xylazine was used (1:0.05 ratio). Animals weighing less than 30 kg were only immobilized with ketamine (0.2 ml/kg) and were handled without being fully anesthetized. Finally, captured animals were fitted with ear-tag radiotransmitters (Advanced Telemetry Systems, Isanti, Minnesota, and Wagener Telemetrieanlagen, Cologne, Germany). Procedures used for capture and

immobilization followed guidelines of the American Society of Mammalogists (Sikes et al. 2011), and our research and handling protocol was approved by the Local Ethical Commission for Experiments on Animals in Białystok and Cracow, Poland.

Upon capture, wild boars were classified as juveniles (<12 months old; hereinafter referred to as juv.), subadults (12–24 months; referred to as subad.), or adults (>24 months; referred to as ad.) dependent on tooth eruption (Matschke 1967). However, because trapping mainly took place during winter months, when some animals were about to enter the next age class, individuals were assigned to their respective age classes during the tracking period for analytical purposes (e.g., juveniles captured at age of 10 months and tracked for 7 months would be considered as subadults). A total of 35 wild boar was radiotagged (BPF: 9 ad. and 8 subad. females, 3 ad. and 9 subad. males; Cracow: 2 ad. and 1 subad. females; 2 ad. and 1 subad. males), 26 of which belonged to 7 marked social groups (BPF: 24 ind. in 6 groups; Cracow: 2 ind. in 1 group). The remaining 9 individuals (BPF: 5; Cracow: 4) were either solitary or members of unmarked groups.

Radiotagged individuals were located 2–4 times per week with equal intensity during the day and night (G-test: $G_1 = 0.48$, $P = 0.49$). Consecutive locations were separated by at least 12 h to ensure independence of observations (Swihart and Slade 1985). The locations of individuals were determined on foot by recording at least 3 bearings for each triangulation using a 3-element Yagi antenna (Titley Scientific, Lawnton, Australia) and Yaesu FT-817 transceiver (Yaesu Musen Co., Tokyo, Japan). A vehicle was used to move about the study areas. The location of an individual was calculated from a given set of bearings and using the maximum likelihood estimator method described by Lenth (1981). Only location estimates with error ellipse ≤ 2 ha were included for further analysis, and the program LOAS (Ecological Software Solutions) was used to calculate positions from triangulation. Accuracy of triangulation was determined in the field by locating transmitters in known location (Harris et al. 1990). Mean estimated error between the known transmitter location and those obtained from telemetry was 153 ± 107 m ($\bar{X} \pm SD$, $n = 120$).

Throughout the study tagged individuals were monitored during 24-h continuous tracking sessions, when both location and the activity of individuals were recorded at 30-min intervals. Animals were tracked by a single person (6-h shifts) taking bearings approximately every 10 min from forest roads (BPF) or streets and park trails (Cracow). Continuous tracking followed methodology used by Kamler et al. (2007a,b). Individual activity was determined by assessing irregularities in signal strength when each bearing was taken (Boitani et al. 1994; Kenward 1987; Keuling et al. 2008a; Massei et al. 1997). Researchers listened to the signal for 1 min and classified wild boar as active if the signal was alternating in strength, or inactive when the signal was constant. Direct observations of radiotagged individuals confirmed that changes in signal strength were attributed to both traveling and on-site activity

(e.g., foraging), whereas constant signals indicated a lack of movement (e.g., resting).

Data analysis.—Wild boars were followed for 9.7 ± 3.16 ($\pm SD$, $n = 34$, min = 6, max = 18) months (BPF: 9.5 ± 2.8 , $n = 29$; Cracow: 11.0 ± 5.1 , $n = 5$) and 86 ± 39.4 (min = 35, max = 177) locations were collected per individual (BPF: 74 ± 27.7 , Cracow: 153 ± 28.8). To avoid underestimation of home range size, only those individuals tracked for >3 months and that yielded >30 locations were used in analyses. Using this threshold value we found no effect of increased tracking time or number of locations on home range size (Spearman's $r = 0.06$, $n = 34$, $P = 0.74$ and $r = 0.04$, $P = 0.81$, respectively).

We estimated home range size using two methods: local-convex-hull (LoCoH—Getz and Wilmer 2004) and minimum convex polygon (MCP). The LoCoH method has an advantage over classical methods, e.g., MCP, because hard boundaries and inaccessible areas within the home range (e.g., rivers, highways, buildings) are identified (Getz et al. 2007; Huck et al. 2008). Thus, home ranges are constructed in such a way that only the areas truly utilized by animals were included, which is of great importance for accurate estimation of home ranges in fragmented habitats, e.g., urban or agricultural areas. However, we included results obtained with MCP to allow for comparison with other studies (Table 1). Specifically, the adaptive LoCoH method (*a*-LoCoH) was used, because it is remarkably robust to deviations from the optimal value of the parameter *a*, and, compared with other LoCoH methods, is considered to be the superior method of estimating home range size (Getz et al. 2007). Value of *a* parameter was set at the greatest distance between any 2 points in a set of an individual's locations, as suggested by Getz et al. (2007). Huck et al. (2008) showed that *a*-LoCoH estimates home range size reliably with number of locations comparable with our sample sizes. Ninety percent isopleths were used for home range estimation as it was recently demonstrated that using isopleths greater than 90% can result in unreliable area estimates biased by sample size and sensitive to outliers (Börger et al. 2006).

During the study, 26 wild boars were monitored 71 times during continuous, 24-h tracking sessions. The number of sessions was distributed evenly across sex and age classes (ad. M: 20; subad. M: 15; ad. F: 20; subad. F: 16). Seasons were defined as winter (December–February), spring (March–May), summer (June–August), and autumn (September–November) to reflect changes in climate, vegetation, and life cycle of wild boar. Continuous tracking was conducted during every season (winter: 12 sessions; spring: 23; summer: 17; autumn: 17). Using data collected from 24-h tracking sessions, the following parameters of the daily behavior were calculated: daily range size: using *a*-LoCoH and MCP. All locations were used under the assumption that they would reflect the actual area utilized within the 24-h period; daily distance traveled: sum of distances between consecutive locations; duration of activity: sum of active readings recorded at 10-min intervals (assuming each active reading = 10 min) over the 24-h period; diurnality: proportion of active readings during daylight (time from

Table 1.—Mean values of home range size, daily range size, daily distance traveled, duration of activity, and diurnality of wild boar (*Sus scrofa*) in Cracow City and Białowieża Forest study areas, Poland, during 2006–2008.

	Białowieża Primeval Forest			Cracow City			<i>P</i> -value ^a
	<i>n</i> ^b	$\bar{X} \pm SD$	Min–max	<i>n</i>	$\bar{X} \pm SD$	Min–max	
Home range size (km ²)							
<i>a</i> -LoCoH 90%	29	2.2 ± 0.94	0.8–4.6	5	1.0 ± 0.60	0.6–2.1	0.044
MCP 90%	29	4.2 ± 2.51	0.9–9.9	5	3.9 ± 3.16	1.0–8.7	–
Daily range size (km ²)							
<i>a</i> -LoCoH 100%	20 (35)	1.0 ± 0.73	0.1–3.6	6 (36)	0.9 ± 0.64	0.1–2.5	–
MCP 100%	20 (35)	1.3 ± 1.36	0.1–7.3	6 (36)	2.4 ± 2.19	0.1–8.8	–
Daily distance traveled (km)	20 (35)	6.8 ± 2.56	2.5–16.4	6 (36)	12.9 ± 6.51	3.1–26.7	0.002
Activity duration (h/day)	20 (35)	11.2 ± 5.23	3.3–22.8	6 (36)	11.4 ± 1.70	7.2–14.9	0.299
Diurnality ^c	20 (35)	0.52 ± 0.24	0.0–1.0	6 (36)	0.1 ± 0.08	0.0–0.3	<0.001

^a If shown, *P*-value refers to parameter Area in the most parsimonious model for the given response variable.

^b Number of animals, in parentheses: number of 24-h continuous tracking sessions.

^c Percent of active fixes during daylight hours.

sunrise to sunset) compared with the total number of active readings during each 24-h period. Data were controlled for seasonal changes in day length, daylight-saving time changes, and difference of sunrise and sunset time between the study areas. Finally, the distribution of activity and speed of movement throughout the day were investigated in both study areas. For such analysis, data were pooled into 2-h intervals before the percentage of active locations and cumulative distances traveled was calculated for each interval within both study areas. All spatial and home-range analyses were conducted using R version 2.13.1 software (R Development Core Team 2011) and visualized in Arc View GIS 9.1 (ESRI, Redlands, California).

Statistical analyses.—Linear mixed models (Pinheiro and Bates 2000) were used to analyze relationships between dependent variables (home range size, daily range size, daily distance traveled, and duration of activity) and explanatory variables (study area, season, sex, and age of individuals). Factor “study area” incorporated differences between study areas due to combined effect of human pressure (human presence and activity, habitat structure). Mixed models were used because of the nonindependent nature of the data. When fitting models to home range size data, group ID was treated as a random factor because some individuals belonged to the same social groups (see subsection “Trapping and radiotracking”). Similarly, in models used to analyze variables derived from continuous tracking sessions, individual ID was treated as a random factor because numerous animals were sampled more than once (on average, 2.9 sessions/ind.). The distribution of model residuals was checked for normality using the Shapiro–Wilk test. Data on daily range size were log-transformed to improve normality and reduce skewness. Diurnality data (proportion of active fixes during daytime) were arcsin transformed. Interactions between explanatory variables were included in each model. Akaike information criterion (AIC), with a second-order correction for small sample size (AIC_c), was used to rank models dependent on their fit (Burnham and Anderson 2002). Models with the lowest AIC_c values were considered to be the best-fit models, and models within 2 AIC_c units were considered of similar

quality to the most parsimonious model. All statistical analyses were conducted using R version 2.13.1 software (R Development Core Team 2011).

RESULTS

Spatial behavior.—Home range size estimates obtained using *a*-LoCoH and MCP were highly correlated, both in total home range and daily range (Spearman’s $r = 0.73$, $n = 34$, $P < 0.001$ and $r = 0.80$, $n = 71$, $P < 0.001$, respectively). Therefore, we restricted further analysis only to *a*-LoCoH estimates because they reflect area actually used by wild boar.

In Cracow City, average home range was less than half the size of that in BPF (Table 1). Variation in home range size of wild boar was best explained by differences between the 2 study areas (Tables 2 and 3). The model including only study area as an explanatory variable explained the variation in home range size better than other models, and accounted for 41% of the model weight (Table 2).

On a daily basis wild boar utilized areas of similar size in each study area (Table 1). However, in Cracow City daily occupied range constituted 90% of the total home range, whereas in BPF the daily range only covered 45% of the total home range. None of the explanatory variables sufficiently explained variation in daily range size. Consequently, the intercept-only model provided the best fit (Tables 2 and 3).

In Cracow City, daily distance traveled by wild boar was almost twice that of wild boar within the BPF (Table 1). On average, subadult wild boar covered 65% longer distances on a daily basis compared with adults ($\bar{X} \pm SD$; 12.6 ± 6.51 km, 8.1 ± 4.52 km, respectively). In Cracow City distances covered daily were lower during the spring compared with other seasons, whereas in BPF, contrastingly, daily movement distance was consistent during all seasons (Fig. 2a). The best model explaining variation in daily distance traveled included study area, age, season, and an interaction between study area and season (Table 2). Although overall effect of season was insignificant in the best model (Table 3), different seasonal effects between the study areas were identified, as indicated by a significant interaction term (Table 3).

Table 2.—Confidence set of mixed linear models ($\Delta AIC_c < 2$) for variables explaining home range size, daily range size, daily distance traveled, duration of activity, and diurnality of wild boar (*Sus scrofa*) in Cracow City and Białowieża Primeval Forest study areas, Poland studied in 2006–2008. Included in the table are corrected Akaike information criterion (AIC_c) values and the difference between each model and the best-fitting model (ΔAIC_c), number of model parameters (k), and model Akaike's weights (ω_i). The models were ranked dependent on the AIC_c value and in descending order (the most parsimonious models are on the top of each list).

Response variable	Variables included in a model	k	AIC_c	ΔAIC_c	ω_i
Home range size	Area	4	79.98	0	0.412
	Area + Age	5	81.23	1.25	0.220
	Area + Sex	5	81.56	1.58	0.187
	Area + Age + Sex	6	81.64	1.66	0.180
Daily range size	Intercept	3	69.80	0	0.355
	Age	4	70.69	0.89	0.227
	Sex	4	71.64	1.84	0.141
	Area + Season + Area \times Season	10	71.65	1.85	0.140
Daily distance	Area	4	71.70	1.90	0.137
	Area + Age + Season + Area \times Season	11	1,361.74	0	0.484
	Area + Age + Season	8	1,362.55	0.81	0.322
Activity duration	Area + Age + Season + Sex + Area \times Season	9	1,363.58	1.84	0.193
	Season + Area + Area \times Season	10	363.56	0	0.404
	Season + Area + Age + Area \times Season	11	364.87	1.31	0.210
	Season + Area + Sex + Area \times Season	11	364.97	1.42	0.199
Diurnality	Season	6	365.10	1.55	0.187
	Area + Season + Area \times Season	10	-383.54	0	0.342
	Area + Season + Age + Area \times Season	11	-383.40	0.13	0.320
	Area + Season + Sex + Area \times Season	11	-382.29	1.25	0.183
	Area + Season + Age + Sex + Area \times Season	12	-381.95	1.59	0.155

Table 3.—Parameters and their statistics included in the most parsimonious model from the confidence set of models ($\Delta AIC_c < 2$), and with home range size, daily range size, daily distance traveled, duration of activity, and diurnality of wild boar (*Sus scrofa*) as response variables. All explanatory variables were factors and estimates for factor levels are presented in relation to: area (Białowieża), season (winter), and age (adult).

Response variable	Parameter	Coefficient	SE	t -value	P -value
Home range size	Intercept	2.29	0.27	8.44	<0.001
	Area (Cracow)	-1.20	0.54	-2.23	0.044
Daily range size	Intercept	-0.16	0.047	-3.52	<0.001
Daily distance	Intercept	4,648.3	2,491.64	1.86	0.069
	Area (Cracow)	9,775.4	2,856.52	3.42	0.002
	Age (Subadult)	2,978.5	1,092.78	2.72	0.009
	Area (Cracow \times spring)	-8,074.1	3,380.86	-2.39	0.022
	Area (Cracow \times summer)	-5,314.7	3,642.97	-1.46	0.153
	Area (Cracow \times autumn)	-3,708.0	3,587.29	-1.03	0.307
	Season (autumn)	3,075.6	3,024.32	1.02	0.315
	Season (summer)	1,465.4	2,757.31	0.53	0.598
	Season (spring)	460.8	2,761.82	0.17	0.868
	Activity duration	Intercept	9.61	1.80	5.33
Season (autumn)		6.14	2.04	3.01	0.004
Area (Cracow \times autumn)		-6.73	2.30	-2.91	0.005
Area (Cracow \times spring)		-3.55	2.09	-1.70	0.096
Area (Cracow \times summer)		-3.81	2.25	-1.69	0.098
Season (spring)		2.82	1.78	1.58	0.121
Area (Cracow)		2.58	2.42	1.07	0.299
Diurnality	Season (summer)	0.78	1.81	0.43	0.666
	Intercept	0.058	0.0056	10.31	<0.001
	Area (Cracow)	-0.053	0.0071	-7.45	<0.001
	Season (summer)	0.054	0.0089	6.05	<0.001
	Season (spring)	0.044	0.0088	4.91	<0.001
	Area (Cracow \times summer)	-0.043	0.0117	-3.68	<0.001
	Area (Cracow \times autumn)	-0.039	0.0115	-3.39	0.002
	Season (autumn)	0.030	0.0097	3.05	0.004
	Area (Cracow \times spring)	-0.026	0.0108	-2.42	0.021

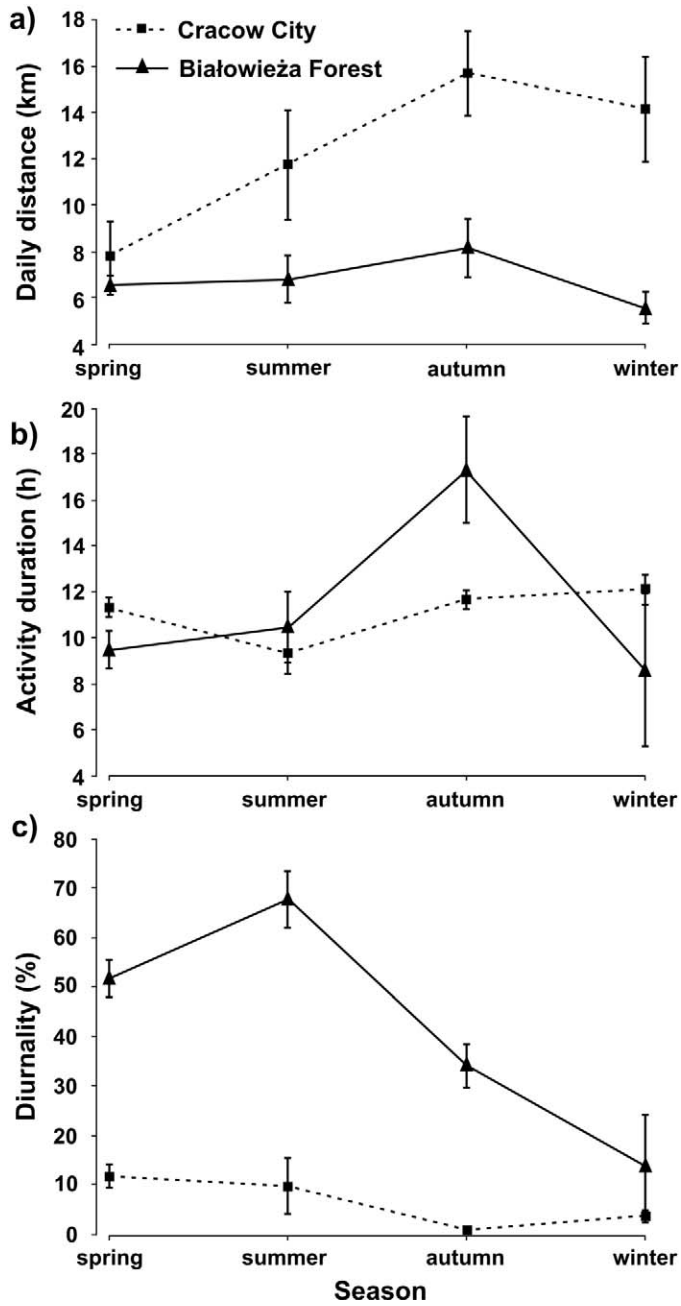


Fig 2.—Seasonal changes in mean values ($\pm SE$) of a) daily distance traveled, b) duration of activity, and c) diurnality (proportion of active fixes taken during daylight hours from total number of active fixes during 24-h period) of wild boar (*Sus scrofa*) in Cracow City and Białowieża Primeval Forest study areas during 2006–2008.

Activity patterns.—Variation in duration of activity was largely driven by seasonal changes and the different effects of season in the 2 study areas (Tables 2 and 3). Specifically, seasonal variation in the duration of activity was a result of the wild boar in BPF being active for longer periods (by 5.7 h on average) in autumn compared with Cracow City (Fig. 2b, Table 3). During other seasons duration of activity was comparable between study areas (Fig. 2b, Table 3). Overall, differences

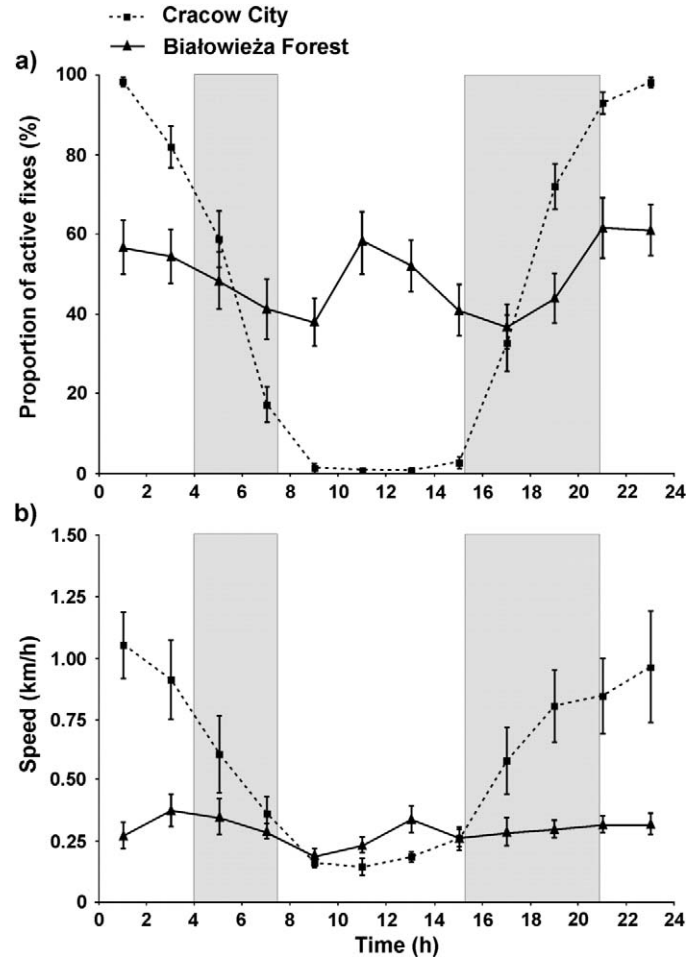


Fig 3.—Distribution of a) activity and b) speed of movement during 24-h period of wild boar (*Sus scrofa*) in Cracow City and Białowieża Primeval Forest study areas during 2006–2008. Mean ($\pm SE$) values are shown for 2-h time intervals. Shaded areas represent the shifting times for sunrise and sunset throughout the year.

between study areas did not contribute significantly to explained variation in activity duration (Tables 2 and 3).

Wild boars in BPF were more active during daylight compared with Cracow City, where they were virtually inactive during daylight (Fig. 3a, Table 1). Study area, season, and an interaction between study area and season were included in the best model describing variation in diurnality (Table 2). Furthermore, seasonal changes in diurnality contributed significantly to explained variation of this parameter (Fig. 2c, Table 3). Effect of season on daytime activity was particularly strong in BPF, with the lowest values observed during winter (Fig. 2c, Table 3).

In BPF, activity was evenly distributed throughout the 24-h period (Kruskal–Wallis $H_{11,409} = 18.16$, $P = 0.078$; Fig. 3a), whereas in Cracow City activity was concentrated to crepuscular and dark hours (Kruskal–Wallis $H_{11,421} = 375.98$, $P < 0.001$; Fig. 3a). A similar pattern was observed with regard to speed of movement. Movements were uniformly distributed throughout the day in BPF, but not in Cracow City (Kruskal–Wallis $H_{11,409} = 15.13$, $P = 0.18$; $H_{11,421} = 106.01$, P

< 0.001, respectively; Fig. 3b). Finally, the proportion of active fixes within 2-h intervals in Cracow City was correlated with the speed of movement (Spearman's $r = 0.97$, $P < 0.001$), whereas in BPF, activity was not significantly associated with movement (Spearman's $r = 0.44$, $P = 0.15$).

DISCUSSION

This study demonstrated high behavioral plasticity in wild boar living in 2 contrasting areas differing in human pressure, both direct human presence and indirect human-induced habitat changes. Wild boar inhabiting urban areas occupied smaller home ranges, were more mobile on a daily basis, and were more nocturnal when compared with the population inhabiting a primeval forest characterized by low levels of human pressure. In contrast, daily duration of activity and daily range size were comparable between both study areas. Some behavioral parameters (daily distance traveled, activity duration, and diurnality) were affected by seasonal changes, although the effects were different in the 2 study areas. Seasonal effects were stronger in the BPF compared with the urban area of Cracow City. However, because our study was based on a relative small number of individuals that were also unevenly distributed between the study areas, our results should be interpreted with caution.

Spatial behavior in areas with low and high human pressure.—In contrast to the continuous forest habitat of BPF, the urban area of Cracow City provides patchy habitat with dispersed resources (e.g., food, resting, and breeding sites). This difference in habitat structure most likely contributed to contrasting spatiotemporal patterns observed between both study areas. Within the urban environment wild boar had to cover distance almost twice as long as those in primeval forest to meet their daily energetic requirements, as well as to locate shelter for long periods of diurnal inactivity. Interestingly, wild boar showed similar seasonal patterns in both areas, except during spring when a reduction in daily distance traveled was observed in Cracow City. Spring is the breeding season for wild boar (Fernandez-Llario and Carranza 2000; Jędrzejewska and Jędrzejewski 1998) and restricted daily movement could be a result of parturition and weaning of offspring (females yielded 65% of data for this season), as detailed in Spitz and Janeau (1990).

Wild boar is a generalist omnivore with opportunistic feeding habits, and its diet reflects local environmental conditions (Herrero et al. 2006; Schley and Roper 2003). Consequently, wild boar can take advantage of a variety of food resources offered by urban environments (e.g., crop fields, metropolitan parks and forests, garbage dumps, and orchards). In contrast to BPF, where food abundance is seasonally variable (Jędrzejewska and Jędrzejewski 1998), urban environments provide relatively high and constant food resources, which could explain the smaller home ranges observed in Cracow City. Therefore, our result may support the “food-exploitation hypothesis,” which predicts an inverse relationship between food abundance and home range size (Larter and

Gates 1994). However, in this study we did not quantify food resource abundance. Besides food abundance, habitat fragmentation could also contribute to smaller home ranges observed in the urban area.

Wild boar in BPF occupied daily ranges that constituted less than half (45%) of their total home range, whereas in Cracow City almost the entire home range (90%) was covered on a daily basis. A potential explanation could be that wild boar in the BPF shift their ranges spatially according to spatiotemporal changes in food resources, which is similar to shifts described by Keuling et al. (2009) for wild boar in Germany.

No effect of study area, season, sex, or age on daily range size was detected in our study. Other studies have had similar findings, e.g., the lack of seasonal and sexual differences in daily range size were reported in a study from Italy (Russo et al. 1997). However, variation in daily range size may also be shaped by subtle site-specific factors (e.g., daily ambient temperature—Kamler et al. 2007a), which were not included in our group of robust explanatory variables.

Activity patterns in areas with low and high human pressure.—In both study areas wild boars were active for similar periods of time (~ 11 h/day), which suggests that individuals had to balance comparable energy budgets. However, there was a remarkable difference between the distributions of activity throughout the day among the 2 habitats. Wild boar in the urban area exhibited crepuscular and nocturnal activity, which could have been a strategy of avoiding interference with humans. This finding is consistent with other studies investigating urban mammal populations (wild boar in Barcelona, Spain—Cahill et al. 2003; red fox [*Vulpes vulpes*] in Oxford, United Kingdom—Doncaster and Macdonald 1997). Furthermore, activity was strongly associated with movement, which suggests that wild boar visited numerous food patches and spent relatively little time foraging on one patch before finding secluded sites for daytime resting. In contrast, activity of wild boar in the primeval forest was evenly distributed throughout the 24-h period and showed a polyphasic pattern characterized by alternating phases of activity and resting. Interestingly, similar patterns have been found in other ungulates inhabiting BPF (red deer—Kamler et al. 2007b; European bison—Caboń-Raczyńska et al. 1987). However, in those species the alternating peaks of activity and resting are attributed to the foraging habits of ruminants (food intake and regurgitation), which is not the case in wild boar. High level of diurnality observed in the BPF was possibly caused by very limited hunting pressure in this area, as it had been shown that high hunting pressure increased nocturnal activity of wild boar (Keuling et al. 2008a). Thus, observed activity patterns, as well as high activity during daylight hours, are likely a consequence of low levels of human activity. Wild boar in the BPF showed mainly on-site activity, as suggested by a nonsignificant relationship between activity and speed of movement, and this can be explained by uniformly distributed and readily available resources (food, water, and resting sites) that minimize the need for extensive movement.

Wild boars from BPF were active for exceptionally long periods during the autumn when compared with other seasons, as well as to Cracow City. Two interacting factors may be responsible for this pattern. First, the severity of winter has been shown to be a main factor affecting survival and reproduction of wild boar (Geisser and Reyer 2005; Jędrzejewska and Jędrzejewski 1998). Therefore, achieving good body condition and gaining fat reserves before winter is crucial for wild boar survival. Second, the acorn crop occurring in autumn is the most efficient way to obtain sufficient fat reserves within the BPF (Jędrzejewska and Jędrzejewski 1998), explaining the higher activity observed in autumn. In contrast, no seasonal effect was observed for this parameter in Cracow City, which may indicate that urban environments provide stable, season-independent food resources. Alternatively, the milder climate within the city may reduce the requirement for gaining crucial fat reserves.

In the BPF, wild boar co-occur with 2 natural predators, wolf and lynx. However, predation constitutes a relatively small portion of natural mortality of wild boar in the area, only 19% from wolf and 1% from lynx (Jędrzejewska and Jędrzejewski 1998). Predation risk affects spatiotemporal behavior at various scales and may lead to, e.g., reduced locomotory activity and range size, and changes in habitat use (Borkowski and Owadowska 2010; Valeix et al. 2009). However, literature on spatiotemporal response of wild boar to predation risk is lacking. In our study, we could not quantify the effect of predation and separate it from other factors (low human pressure, habitat structure). Season also had strong effects on the proportion of time wild boars were active during daylight hours (diurnality). This effect was particularly pronounced in the BPF. It was apparent that seasonal changes in levels of diurnality mirrored seasonal changes in day length. Diurnality, with regard to our calculations, was a relative measure giving proportion of the total amount of activity during a 24-h period allocated to daylight hours. Therefore, it is sensitive to varying day length, especially when duration of activity is constant throughout the year, which was found to be the case in our study (except for autumn in the BPF). Overall, levels of diurnal activity within the urban area were much lower than those in the primeval forest (usually below 10% of total daily activity time). Moreover, urban populations maintained nocturnal activity almost irrespective of season, whereas forest population followed natural changes in day length. This difference may demonstrate effect of human pressure on activity patterns of wild boar.

In summary, our study showed that wild boar can adjust their spatiotemporal behavior to local conditions. The spatial behavior and activity of wild boar population inhabiting primeval forest seemed to be mainly driven by seasonal changes in food availability and abiotic conditions, whereas human activity shaped spatiotemporal patterns of the urban population.

Densities of wild boar have been increasing over the last decades within Europe (Apollonio et al. 2010; Geisser and Reyer 2004; Sáez-Royuela and Telleria 1986). Additionally, this expansion is accompanied by invasion of new habitats densely

populated by humans (Cahill et al. 2003; Fisher et al. 2004), including urban areas that may offer new unexplored niches. Several factors have been proposed to explain demographic expansion of wild boar (Bieber and Ruf 2005). Until now, however, behavioral plasticity of the species has not drawn much attention, although it may play an important role in this process.

ACKNOWLEDGMENTS

The project was funded by the Polish Ministry of Science and Higher Education (grant No. 2 P04F 073 29). We are grateful to K. Bojarska, R. Kozak, A. Maszczyk, and many students and volunteers for their help with fieldwork. We also thank the Environmental Engineering Department of Cracow Municipal Office, City Park and Zoological Garden Foundation, and “Podwawelskie” Hunting Club for permission to work in the forested areas of Cracow and help with fieldwork. Statistical analyses were improved thanks to valuable comments from K. Zub and M. Oliver. T. Borowik helped to improve graphics and H. Parris revised English. We are grateful to D. Kuijper and 2 anonymous reviewers for valuable comments on an earlier version of the manuscript.

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Submitted 10 February 2012. Accepted 29 May 2012.

Associate Editor was Harald Beck.