

POSSIBLE USE OF NATIONWIDE DIGITAL SOIL DATABASE ON PREDICTING ROE DEER ANTLER WEIGHT

LEHOCZKI, R.¹, CENTERI, CS.², SONKOLY, K.¹ and CSÁNYI, S.¹

¹*Institute for Wildlife Conservation, Szent István University*

H-2103 Gödöllő, Páter Károly u. 1, Hungary; E-mail: leho@ns.vvt.gau.hu

²*Department of Nature Conservation and Landscape Ecology, Szent István University*

H-2103 Gödöllő, Páter Károly u. 1, Hungary

The overall importance of soil characteristics among habitat components has been recognized for quite a long time as an important factor affecting wildlife. However, spatial analysis between digital soil and wildlife characteristics information were not widely used to specify this connection. Moreover, most related studies in this area have not been using quantitative measures of soil fertility, but instead focusing on general differences among regional soil properties. The purpose of this research was to test the applicability of an intermediate scale digital soil information map in wildlife management on nationwide level using a special soil fertility index and main soil types. Results were reached by completing a spatial analysis of digital soil maps and roe deer (*Capreolus capreolus* LINNAEUS, 1758) antler weight information maps covering the area of Hungary. Using a spatial lag regression model, the simplified method of soil evaluation (soil types) explained more on antler weight variance than the specific soil fertility. Our results indicated that modelling can be more effective with the screening of other influencing factors on antler development, which are inherently linked with soil properties (e.g. vegetation cover). Furthermore, we can point out that higher resolution soil maps do not provide a better explanation for the connection of soil characteristics and antler weight.

Key words: antler weight, map scale, roe deer, soil fertility, soil type

INTRODUCTION

European roe deer (*Capreolus capreolus* LINNAEUS, 1758) is highly important in Hungarian game management (FODOR 1983), thanks to its countrywide distribution, good quality, abundant population and its popularity with hunters (CSÁNYI & LEHOCZKI 2007). Selling buck hunting opportunities, mainly to foreign trophy hunters (MYSTERUD *et al.* 2006) results significant income for game management units (HOFER 2002). Antler weights are the most important parameters in trophy hunting, thus it is substantial to gain wide knowledge about factors influencing antler quality to aid in the development of wildlife management practices.

The development, size and quality of antlers are influenced by numerous factors. It is not fully known which effects have the highest importance. Environmental effects including feeding conditions are considered more important (BROWN 1990, VANPÉ *et al.* 2007) than hereditary characteristics (HARMEL 1982, HARTL *et*

al. 1995). The quality of food is in strong relation with the soil in general, and with its physical and chemical properties in particular (FULLER & AMUNDSEN 1987).

The majority of the articles about soil-wildlife relationships address wildlife damage, ecotoxicology, and soil contamination by heavy metals and other pollutants (e.g., STREBL *et al.* 1996, TATARUCH & KIERDORF 2003, MYSTERUD 2006). BAILEY (1984) summarized the overall importance of soil among habitat components and their effects on the quality of animals. He emphasized the relationship between soil and game populations, highlighting the influential determining effects of soil in game management. The positive relationship among general soil conditions and deer population parameters (KLEIN & STRANDGAARD 1972, SMITH *et al.* 1975), and thus antler development (SWEET & WRIGHT 1952, STRICKLAND & DEMARAIS 2000, WAER 2001), was demonstrated with local or regional studies.

In the last few years, STRICKLAND and DEMARAIS (2006) carried out a regional analysis in Mississippi, USA, using GIS tools to examine how a digital soil map and its database could be used to predict white-tailed deer (*Odocoileus virginianus* ZIMMERMANN, 1780) population morphometrics. They concluded that the use of the State Soil Geographic Database to explain variation in deer antler size and body mass due to its spatial resolution (1:250,000 mapping unit 625 ha) and attributive data content, types of soil properties, was limited.

The effects of scale (focusing on measurement unit or grain, not on the extent, see TURNER *et al.* 1989) on ecological patterns were investigated e.g. in connection to sexual segregation (BOWYER *et al.* 1996) and range size of deer (WALTER *et al.* 2009). For example, WALTER *et al.* (2009) found differences in model selection for 4 hierarchically created maps (with different spatial grain) to reflect levels of landscape connectivity when studied how variability of habitat conditions could influence range size. TURNER *et al.* (1989) pointed out that characterising the relationships between ecological measurement and the grain (or extent) of the data may make it possible to predict or correct for the loss of information with changes in spatial scale. BOWYER and KIE (2006) emphasized that biological processes can either reduce or enhance scale-sensitive phenomena.

Based on the above-mentioned findings about the importance of map resolution and the soil properties used in the present work, the authors test the following predictions:

(1) Soil fertility, which probably has the highest importance on the roe deer forage (BAILEY 1984), could explain more variance in antler weight than soil types, which may be considered the most general soil characteristic among the soil properties.

(2) The intermediate scale soil information map, due to its higher (1:100,000) resolution, could explain more variation in antler weight data.

MATERIALS AND METHODS

Soil data

The Agrotopography Map (ATOPO, scale of 1:100,000) was used for our analyses. ATOPO was prepared by the Hungarian Academy of Sciences, Research Institute of Soil Science and Agricultural Chemistry, based on pedological, meteorological, and land use data (VÁRALLYAY 1985, 1995). The pedological background of ATOPO mainly relies on Kreybig-type soil information maps (available for the whole area of Hungary at the scale of 1:25,000) and the soil maps of the former co-operatives (prepared for arable lands at the scale of 1:10,000 between 1960 and 1975). Kreybig maps are the results of fieldwork and laboratory measurements fulfilled between 1935 and 1955 (KREYBIG 1937). The Kreybig-type map includes the physical and chemical information from soil drilling points and soil profiles, the latter for each soil genetic layer. The soil maps of arable areas (scale of 1:10,000) include a genetic soil map, a cartogram (including parameters such as pH, soil organic matter, nitrogen, phosphorous and potassium content, hydrology) and a text describing the data. This information was compiled and updated by new field and laboratory measurements during the 1980s and finally resulted in the ATOPO and its digital version.

The thematic layers of ATOPO are as follows: Layer 1 type and subtype of soil; Layer 2 parent material; Layer 3 soil texture; Layer 4 clay mineral associations of soil; Layer 5 hydro-physical properties; Layer 6 soil reaction and carbonate status; Layer 7 organic matter resource; Layer 8 depth of soil; and, Layer 9. soil-evaluation-number. In the present analysis the soil type layer was used because it is well known and it is the most general soil characteristic and it represents all soil data. It is important to state that, according to VÁRALLYAY *et al.* (1980), soil type alone does not describe all soil parameters necessary for determining the fertility of the given soil. To solve this problem we chose soil-evaluation-numbers (SEN) which is a special soil fertility index representing the natural fertility of different soils relative to the fertility of the most fertile soil (VÁRALLYAY 1985). The basis of the calculation of the SEN is the soil subtype. The most fertile soil subtype is the basis that gives the maximum value (100%), and all other subtypes rated relative to it. The SEN of the other varieties of soil subtypes is calculated based on the type of soil properties provided by the other layers of the database for each of the soil subtypes. Consequently SEN (Layer 9) is the result of the consideration of the preceding 8 layers of ATOPO (Layers 1–8), so it incorporates all important physical and chemical properties of the soil. The digital map database (ATOPO) provides the SEN values arranged into 10 categories (Fig. 1).

Based on the data of the ATOPO Layer 1, soil types and subtypes were classified into main soil types (MST) according to SZABOLCS (1966). Main soil types served as a basis for further analysis (Table 1, Fig. 2).

In the present study we did not use the chemical and physical properties of soils from the ATOPO because the database contains the layers of soil types and SEN, and these layers already comprise these properties. Soil types were formed under determining soil forming factors that can be characterized by certain chemical and physical properties (e.g., pH of salt affected soils is above 8.5), and emphasizing the importance of one single chemical or physical property can be misleading (e.g., salt affected soils have high soil organic matter content but its high salt content reduces fertility).

Antler measurement data

In Hungary, all the antlers of harvested roe deer bucks were measured (weight, different lengths and circumferences) and evaluated based on the International Council for Game and Wildlife

Table 1. The area percentage of the main soil types in Hungary.

Main soil types	Proportional area in Hungary (%)
Skeletal soils ^a (MST1)	8.2
Lithosols affected by the parent material (MST2)	2.8
Brown forest soils (MST3)	34.3
Chernozem soils (MST4)	22.1
Salt affected soils (MST5)	6.0
Meadow soils (MST6)	21.2
Peaty soils (MST7)	1.4
Soils of swamp forests (MST8)	0.1
Fluvisols and colluvium soils (MST9)	2.7
Total ^b	98.8

^aVery shallow soils with only a very little (<10 cm) 'A horizon' or no horizon at all;

^bThe remaining 1.2% is not classified (lakes and capital)

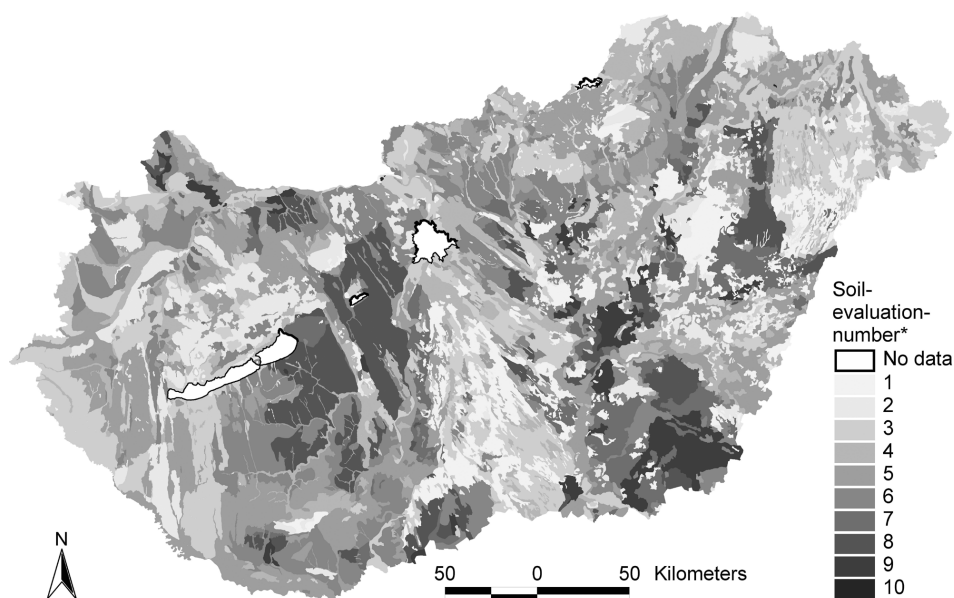


Fig. 1. The values of soil-evaluation-number (representing the natural fertility of different soils in the percentage of the fertility of the most fertile soil) from the Agrotopography Map of Hungary. (* 1, <10%; 2, 10–20%; 3, 20–30%; 4, 30–40%; 5, 40–50%; 6, 50–60%; 7, 60–70%; 8, 70–80%; 9, 80–90%; 10, 90–100%). Source: Hungarian Academy of Sciences, Research Institute of Soil Science and Agricultural Chemistry

Conservation (CIC) trophy scoring formula (WHITEHEAD 1981). The data of the evaluated antlers were collected and stored by the National Game Management Database of Hungary (NGMD). The replicate was the game management unit (GMU). The country was divided into 1,198 GMUs and data were available for 1,195 units. Between 1997 and 2006 a total of 234,185 antler observations were recorded. We used antler weight data from bucks older than one year and younger than 8 years ($n = 202,344$) to exclude the effects of high variations of yearling and senescent trophies. Data of bucks harvested between 1997 and 2006 were used because the Hungarian game management planning system is based on 10-year periods. The mean of the ten-year antler weight data for each of the 1,195 GMUs was used in the analysis. We used 10-year means instead of the complete dataset to sort out the effects of changes in weather conditions during the years on antler development (CSÁNYI & SONKOLY 2003, MYSTERUD *et al.* 2005). The NGMD managed and provided the digital GMU map (Fig. 3).

Population data

Densities based on the estimated spring population size and harvest ratios as a proportion of harvested numbers and estimated numbers (collected by NGMD) of roe deer were calculated for each of the GMUs. Means of the ten-year (1997–2006) population data for each of the 1,195 GMUs were used. These data were serviceable to control the effects of population density (density dependence, e.g. VANPÉ *et al.* 2007) and hunting pressure (harvest ratio) on antler development. Harvest ratios were used because, in the case of a higher harvest rate, the proportion of smaller antlered bucks is higher in the cull in Hungary (CSÁNYI & SZIDNAI 1994).

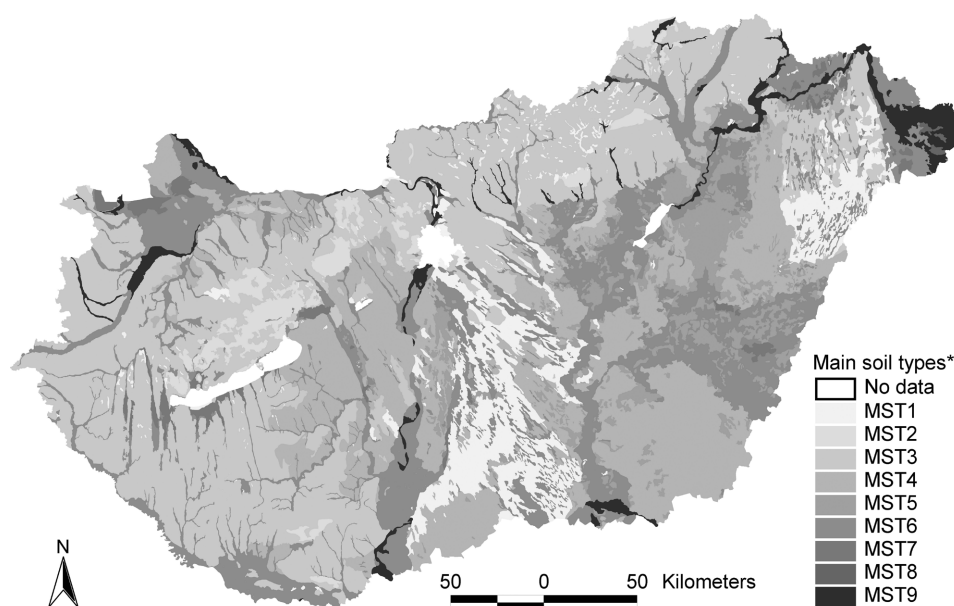


Fig. 2. The spatial distribution of main soil types, based on the soil types and subtypes from the Agrotopography Map of Hungary. (* For abbreviations see Table 1). Source: Hungarian Academy of Sciences, Research Institute of Soil Science and Agricultural Chemistry

Antler data were based on animals harvested by hunters, and the game managers provided the population data which may have influenced the sample (MYRBERGET 1988). It was assumed that the data were similarly biased, and the values were comparable with each other.

Landscape data

Landscape information from the Hungarian CORINE Land Cover 2000 database (CLC2000) was used (prepared by the Institute of Geodesy, Cartography and Remote Sensing, Hungary). The Hungarian CLC2000 was made as a part of European Image 2000 and CORINE Land Cover 2000 Project. The creation of the CLC2000 was based on the interpretation of satellite images with 100 m positional accuracy and 0.25 km² minimum mapping unit. From the 5 main land-use and cover classes, only the information of the agricultural areas and the forestlands were used (excluded classes were artificial, hydrous and water surfaces). The agricultural and forest cover data was suitable for controlling the effects of different land-use, land cover, and habitat types on the antler size (MIRANDA & PORTER 2003).

Spatial analysis

For spatial analysis ArcGIS software (Environmental System Research Institute, Redlands, California, USA) was used. In our study we used the territory of the GMUs as observation units on which the game management data (antler weights, population and harvested numbers) were given. Soil and land cover data were managed with GIS tools to refer them to these GMUs. We intersected the GMU maps with the soil and the land cover maps. Finally, the database contained the area proportions of the 9 main soil types (%), the average soil fertility values (%) and the area proportions of agricultural lands (%) and forest edge length (km/km²) as well as the antler and population data for each of the 1,195 GMUs (Table 2).

Statistical analysis

The statistical tests were performed with the SPSS for Windows (SPSS, Chicago, Illinois, USA), ArcGIS, and GeoDa (ANSELIN *et al.* 2006) software.

The area proportion of the 9 main soil types showed high multicollinearity using the ArcGIS OLS (Ordinary Least Squares) regression function. The calculated Variance Inflation Factor (VIF) values were higher than 5 (HUNYADI & VITA 2008). To solve this problem we used the robust classification tree analysis (in SPSS) for preselection of variables (BREIMAN & FRIEDMAN 1985, SPSS 2004). In order to keep any of the important variables we summarized the area proportions of the main soil types which have positive (MST 4 + 5 + 6 = MST456) and those which have negative effects (MST 1 + 2 + 3 = MST123) on antler weight (Fig. 4), and we discarded those which had no considerable effect (MST 7 + 8 + 9). As the multicollinearity between the MST123 and MST456 variables still remained (VIF = 9.03) we included them only separately in regression models.

In global regression models, such as OLS, and even in GWR (Geographically Weighted Regression) which build a local regression equation for each feature in the dataset (MITCHELL 2005) the models' residuals showed spatial autocorrelation. The Moran's Indexes (Moran's I), which are commonly used to assess spatial autocorrelation in the residuals, were between 0.3 and 0.7 ($P \leq 0.001$), depending on the model, where -1 indicating perfect dispersion, +1 perfect correlation, and zero values a random spatial pattern (ANSELIN 1999).

Table 2. Descriptive values of the variables included in statistical analyses: antler weight, roe deer density (D), roe deer harvest rate (HR), proportional area of agricultural field (AGR), forest edge length (FEL), soil fertility values (SEN), and area proportions of the 9 main soil types (MST1–MST9, for abbreviations see Table 1) in the 1,195 game management units of Hungary.

Variables	n	Mean	SE	SD	Minimum	Maximum
Antler weight (g)	1195	279.13	1.01	34.96	172.86	390.40
D (roe deer/km ²)	1195	3.51	0.05	1.64	0.19	12.64
HR (%)	1195	0.23	0.00	0.09	0.04	0.70
AGR (%)	1195	74.08	0.58	20.10	0.01	100.00
FEL (km/km ²)	1195	0.85	0.02	0.73	0.00	8.26
SEN (%)	1195	41.30	0.45	15.43	6.13	85.00
MST1 (%)	1195	8.41	0.57	19.64	0.00	100.00
MST2 (%)	1195	2.44	0.32	11.21	0.00	95.14
MST3 (%)	1195	37.29	1.14	39.43	0.00	100.00
MST4 (%)	1195	20.57	0.93	32.01	0.00	100.01
MST5 (%)	1195	4.66	0.36	12.28	0.00	97.15
MST6 (%)	1195	22.01	0.75	26.09	0.00	100.00
MST7 (%)	1195	1.36	0.22	7.62	0.00	99.52
MST8 (%)	1195	0.10	0.04	1.53	0.00	32.37
MST9 (%)	1195	2.81	0.29	10.11	0.00	94.52

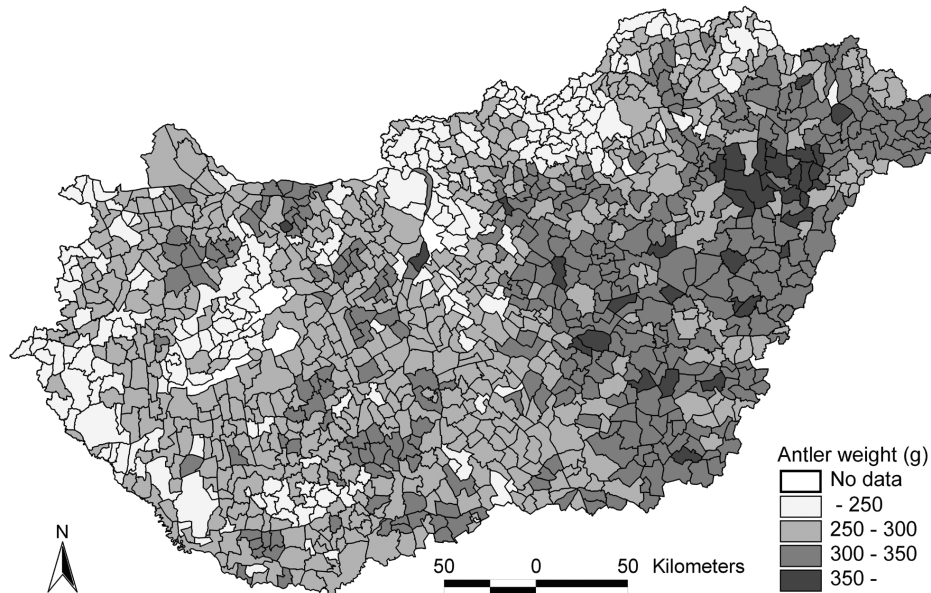


Fig. 3. The ten-year mean values (1997–2006) of roe deer antler weights for each game management unit in Hungary. Source: National Game Management Database of Hungary

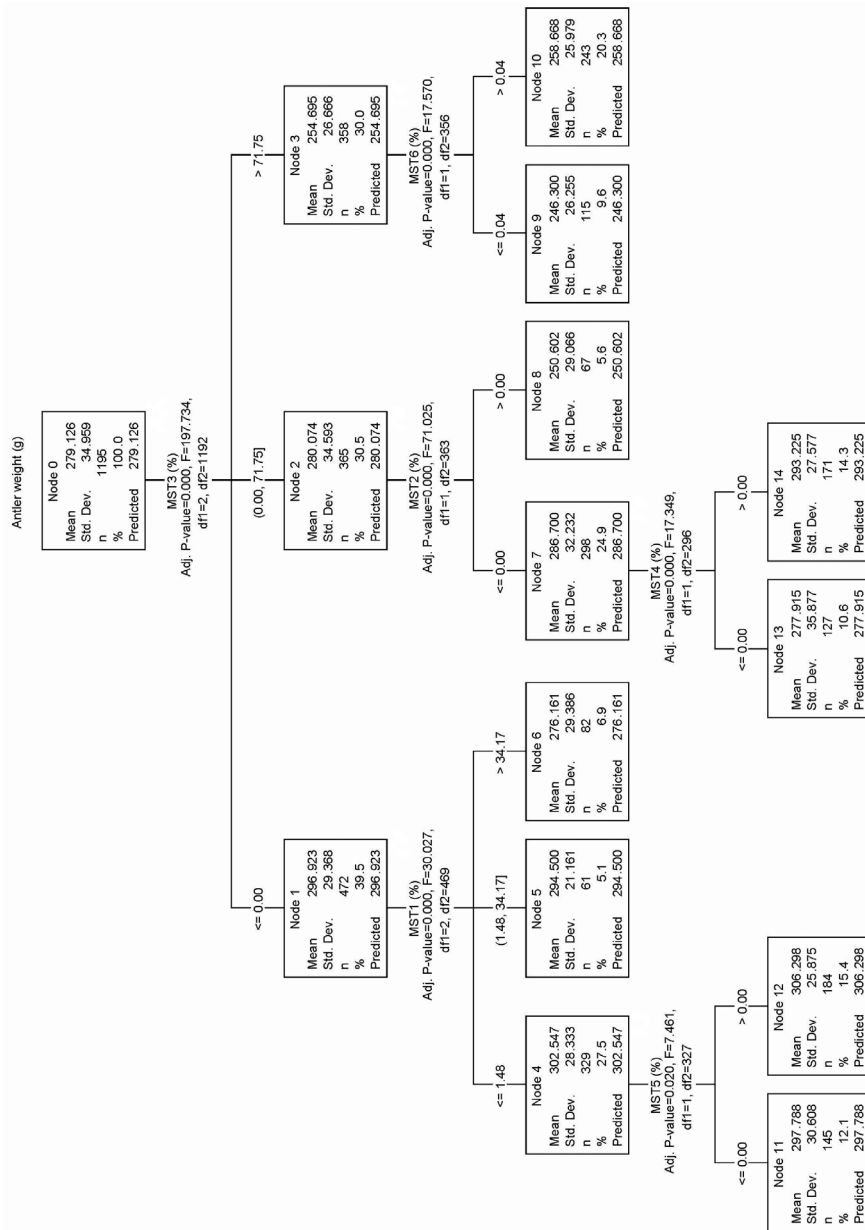


Fig. 4. Results of the classification tree analysis used for preselection of main soil type (MST*) variables based on their effect on antler weight. (* For abbreviations see Table 1)

Because of the presence of spatial dependence we re-estimated the models with the GeoDa software's Spatial Lag Model (SLM) to control for the spatial dependence. In SLM a spatial lag variable was used as a supplementary explanatory variable to control for the spatial dependence. This is the weighted mean of a variable for neighbouring spatial units of the observation unit in question (ANSELIN 1999).

Creating a spatial weight file (higher order queen contiguity) in GeoDa resulted in the model's Moran's I value being reduced to 0.05–0.11 ($P \leq 0.001$).

The spatial lag regression models were used to explain antler weight variation by soil fertility (SEN) alone (SLM I) and by soil types alone (SLM II and SLM III). In SLM II we included MST123 and in SLM III the MST456 as independent variables to check which one has higher explanatory power.

In SLM IV in addition to the soil fertility (SEN), and in SLM V in addition to the soil types (MST123; because they had a higher effect than MST456; see Results), we included a range of potential factors that might influence trophy size besides the examined soil properties such as roe deer population density and harvest rate as well as the proportion of agricultural areas and the length of forest edge.

We used only the above-mentioned environmental factors in the SLM IV and SLM V because our aim was to check the effectiveness of certain soil characteristic to predict the expected antler weight and not to explore all of the environmental factors and their importance in antler development.

RESULTS

Statistical analysis of soil and antler characteristics

Soil fertility in SLM I. explained only 10% of the variation in antler weight (Table 3) and among the 5 models this had the highest AIC value.

The main soil types with positive effects (MST456) in SLM III almost had the same explanatory value (33.1%) as the main soil types with negative effects

Table 3. Spatial lag regression models relating mean antler weight (g) of roe deer to soil types (MST123 – summarized area proportion of skeletal soils, lithosols affected by the parent material, and brown forest soils; MST456 – summarized area proportion of chernozem soils, salt affected soils, and meadow soils) and soil fertility (SEN) as well as roe deer density (D), harvest rate (HR), and land cover information (proportion of the agricultural areas (AGR) and forest edge length (FEL)), using ten-year means in case of trophy and population variables in Hungary, 1997–2006.

Model	Variables	df	K	AIC	R ²
SLM I	SEN	1192	3	11764	0.104
SLM II	MST123	1192	3	11406	0.336
SLM III	MST456	1192	3	11415	0.331
SLM IV	SEN ^a + D + HR + AGR + FEL	1188	7	11059	0.506
SLM V	MST123 + D + HR + AGR + FEL	1188	7	11030	0.518

^a: The SEN does not have significant effect in the model, $P = 0.726$. (df = degrees of freedom; K = number of model parameters; AIC = Akaike Information Criterion; R² = coefficient of determination)

(MST123) in SLM II (33.6%), but based on the models' Akaike values (11415 vs. 11406, respectively) the MST123 were chosen to represent soil types in the SLM V.

In the SLM IV with 50.6% explanatory power, among the independent variables, only the SEN did not have a significant effect ($P = 0.726$) on the model. The SLM V explained 51.8% of the variation in antler weight and this model had the lowest AIC value, providing the best model fit. In SLM V all of the included variables had significant effects on the model.

Examining the R^2 and AIC values of the models shows that the main soil types had higher explanatory effects on the antler weight variation than the soil fertility (Table 3).

For a better interpretation of the results of the main soil types we calculated the average SEN values and the land-use type proportions for each of them (Fig. 5).

DISCUSSION

Soil is a basic element of the natural environment and although it affects antler quality through other environmental factors, generally we managed to show the relation between the two factors with a nationwide digital soil database (ATOPO) at the scale of 1:100,000 in Hungary.

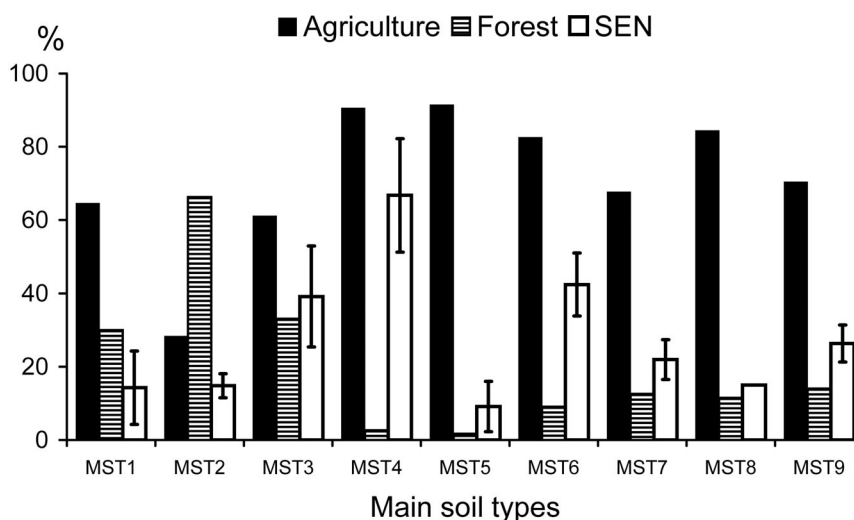


Fig. 5. The means and standard deviations of soil-evaluation-numbers (SEN; soil fertility index representing the natural fertility of different soils in the percentage of the fertility of the most fertile soil) and percentages of land-use types (agriculture and forest) for each main soil types* in Hungary. (* For abbreviations see Table 1)

Contrary to prediction 1, our results suggest that the simplified method of soil evaluation, i.e. soil types, is more sufficient for wildlife management purposes to predict the expected antler weight of roe deer than the specific soil fertility. The general soil evaluation probably comprises information about other factors, which are linked with soil and have an effect on antler development (e.g., different land-use types can be linked to different soil types), which may explain our results.

Related studies in this area seldom use quantitative measures of soil fertility. These works instead are based on general differences among soil conditions. WAER (2001) found differences in the number of antler points and weight of white-tailed deer with varying soil properties in Alabama. SMITH *et al.* (1975) found positive correlation between white-tailed deer body mass and soil fertility ratings. We note that the results of body mass can also be related to antler size as well because it has been demonstrated that antler size increases with body size (VANPÉ *et al.* 2007, GASPAR-LÓPEZ *et al.* 2008). SWEET and WRIGHT (1952) found better white-tailed deer antler qualities connected to better soil fertility. STRICKLAND and DEMARAIS (2000) showed that antler quality and body mass followed soil fertility from best to worst, with the largest antlers growing in the regions characterized by the most fertile soils around the Mississippi River.

Our results also support the work of STRICKLAND and DEMARAIS (2006). They set up a model based on specific soil properties (pH, organic matter, bulk density and available water capacity). They explained as much variation in mean antler size and mean eviscerated body mass values of white-tailed deer as based on simple soil-region classification. They questioned their results because they had concerns over the spatial resolution and accuracy of their values and the spatial distribution of the soil characteristics (1:250,000 scale map, mapping units 625 ha). They also mentioned that applied soil parameters may not affect soil fertility as much as deer forage. Based on their findings the importance of regional differences in soil characteristics are larger than inside the regions connecting to site-specific data with higher spatial resolution. We support their findings on the effects of spatial resolution of the applied soil map database. While our model (soil types alone) based on the 1:100,000 scale map explained 33.6% of antler weight variation, the model of STRICKLAND and DEMARAIS (2006) based on the map of scale 1:250,000 explained 43% of variation in mean antler size. Thus, our prediction 2 also failed. VAN DEN BRINK (2004) also pointed out the importance of spatial scale, mentioning that soil characteristics may vary on a smaller scale than the animals are using in their habitats.

The home range size of white-tailed deer is larger than that which is determined for roe deer, but in both species there are large differences in the age of the individual, habitat, and seasons (DEMARAIS *et al.* 2000, HEWISON *et al.* 1998,

CSÁNYI *et al.* 2003). The relation between the home range sizes of roe and white-tailed deer strengthens our conclusion. Because if the higher resolution soil map would provide better basis for studies of soil–antler correlation, it possibly would be more apparent in case of smaller home ranges.

The results of the main soil types classification show that chernozem, meadow, and salt affected soils provided the best chances for the highest quality of roe deer trophies from the pedological point of view. Whereas areas dominated by skeletal soils, lithosols affected by the parent material, and brown forest soils were associated with lighter weight data of roe deer antlers.

Chernozem soils and meadow soils provide very good habitat for herbivore forage plants with lush vegetation, and in certain periods of the year, especially in springtime, salt affected soils also perform well, providing a high amount of plant species. Based on the pedological characteristics of soils with extremes like skeletal soils and lithosols, the chances of providing adequate forage were not as good as in soils mentioned above.

It was expected that skeletal soils, lithosols affected by the parent material would not perform well, and chernozem, meadow, and salt affected soils would provide the largest antlers. It was unexpected that brown forest soils would result in lower antler weights than salt affected soils; however its fertility was better. The reason for the unexpected results of brown forest soils stems from the dominant land-use types as a higher proportion of brown forest soils covered by forest (Fig. 5). Following this assumption the SLM V soil types, with land use variables and roe deer population data, explained 51.8% from the total variance of antler weight, which is higher than the results of the model including only soil types. This result is not unexpected, as the model includes more independent variables, and we can conclude that considering only soil properties will not provide enough information for reliable wildlife management. Moreover land-use and land cover information appear to have higher effect than soil properties on antler weight variance.

The importance of the effects of land use and the type and structure of the surface cover is supported in several studies (CRAWFORD & MARCHINTON 1989, MYSTERUD *et al.* 2002). KLEIN and STRANDGAARD (1972) found soil quality as a primary factor in determining roe deer density in Denmark, however, they associated the largest body weight to the poorer soils and the smallest deer to the better soils, which is contrary to general findings. They reasoned their results were due to the vegetation determined by soil parameters, differences in land use types (forest or arable land) and in the differences in the density of the deer population.

Comprehensively we can point out that: (1) soil information derived from a soil map with higher resolution will not provide better basis for wildlife management practices than general and regional differences among soil properties. We

can also point out that: (2) besides the survey unit of the soil maps the consideration of other affecting factors from the basic determinative influence of soil has high importance.

*

Acknowledgements – The authors wish to thank the Hungarian Academy of Sciences, Research Institute of Soil Science and Agricultural Chemistry for the permit of using the digital soil database of the ATOPO. We would also like to thank IAN TAPUSKA and MÁRK BESENYEI who improved the English of the manuscript, to PÉTER FEHÉRVÁRI for statistical help, and two anonymous reviewers for comments.

REFERENCES

- ANSELIN, L. (1999) *Spatial econometrics*. School of Social Sciences, University of Texas at Dallas, Richardson, TX, 30 pp.
- ANSELIN, L., SYABRI, I. & KHO, Y. (2006) GeoDa: an introduction to spatial data analysis. *Geographical Analysis* **38**: 5–22.
- BAILEY, J. A. (1984) *Principles of wildlife management*. John Wiley & Sons, New York, 373 pp.
- BOWYER, R. T. & KIE, J. G. (2006) Effects of scale on interpreting life-history characteristics of ungulates and carnivores. *Diversity and Distributions* **12**: 244–257.
- BOWYER, R. T., KIE, J. G. & VAN BALLEMBERGHE, V. (1996) Sexual segregation in black-tailed deer: effects of scale. *Journal of Wildlife Management* **60**: 10–17.
- BREIMAN, L. & FRIEDMAN, J. H. (1985) Estimating optimal transformations for multiple regression and correlation. *Journal of the American Statistical Association* **80**: 580–598.
- BROWN, R. D. (1990) Nutrition and antler development. Pp. 426–441. In: BUBENIK, G. A. & BUBENIK, A. B. (eds): *Horns, pronghorns, and antlers*. Springer-Verlag, New York.
- CRAWFORD, H. S. & MARCHINTON, R. L. (1989) A habitat suitability index for white-tailed deer in the Piedmont. *Southern Journal of Applied Forestry* **13**: 12–16.
- CSÁNYI, S. & LEHOCZKI, R. (2007) Európai őz (European roe deer). Pp. 257–260. In: BIHARI, Z., CSORBA, G. & HELTAI, M. (eds): *Magyarország emlőseinek atlasza. (Atlas of Hungarian mammals.)* Kossuth Kiadó, Budapest [in Hungarian]
- CSÁNYI, S. & SONKOLY, K. (2003) Az őztrófeák nagyságát befolyásoló meteorológiai tényezők értékelése. (The effect of meteorological factors on the antler weights of roe deer.) *Vadbiológia* **10**: 61–67. [in Hungarian with English summary]
- CSÁNYI, S. & SZIDNAI, L. (1994) Őzgazdálkodásunk helyzetének értékelése. (The state of roe deer management in Hungary.) *Vadbiológia* **4**: 73–107. [In Hungarian with English summary]
- CSÁNYI, S., LEHOCZKI, R. & SOLT, SZ. (2003) Az őz területhasználata alföldi, mezőgazdasági élőhelyen. (Space use of roe deer in open, agricultural landscapes in Hungary.) *Vadbiológia* **10**: 1–9. [In Hungarian with English summary]
- DEMARAIS, S., MILLER, K. V. & JACOBSON, H. A. (2000) White-tailed deer. Pp. 601–628. In: DEMARAIS, D. & KRAUSMAN, P. R. (eds): *Ecology and management of large mammals in North America*. Prentice Hall, Upper Saddle River, New Jersey.
- FODOR, T. (1983) Az őz Magyarországon. [Roe deer in Hungary.] Pp. 16–22. In: BERDÁR, B. (ed.): *Az őz és vadászata*. [The roe deer and stalking.] Mezőgazdasági Kiadó, Budapest [In Hungarian]

- FULLER, K. T. & AMUNDSEN, C. C. (1987) Nutritive quality of deer browse related to soil fertility in an oak-hickory forest habitat. Pp. 261–268. *In*: HAY, R. L., WOODS F. W. & DESELM, H. (eds): *Proceedings of the Central Hardwood Forest Conference VI.*, 24–26 February 1987. Knoxville, Tennessee.
- GASPAR-LÓPEZ, E., GARCÍA, A. J., LANDETE-CASTILLEJOS, T., CARRIÓN, D., ESTEVEZ, J. A. & GALLEGU, L. (2008) Growth of the first antler in Iberian red deer (*Cervus elaphus hispanicus*). *European Journal of Wildlife Research* **54**: 1–5.
- HARMEL, D. E. (1982) Effects of genetics on antler quality and body size in white-tailed deer. Pp. 339–348. *In*: BROWN, R. D. (ed.): *Antler development in Cervidae*. Caesar Kleberg Wildlife Research Institute, Kingsville, Texas.
- HARTL, G. B., APOLLONIO, M. & MATTIOLI, L. (1995) Genetic determination of cervid antlers in relation to their significance in social interactions. *Acta Theriologica Suppl.* **3**: 199–205.
- HEWISON, A. J. M., VINCENT, J-P. & REBY, D. (1998) Social organisation of European roe deer. Pp. 189–219. *In*: ANDERSEN, R., DUNCAN, P. & LINNELL, J. D. C. (eds): *The European roe deer: the biology of success*. Scandinavian University Press, Oslo.
- HOFER, D. (2002) *The lions share of the hunt. Trophy hunting and conservation: A review of the legal Eurasian tourist hunting market and trophy trade under CITES*. TRAFFIC Europe, Brussels, 71 pp.
- HUNYADI, L. & VITA, L. (2008) *Statisztika II.* (Statistics II.) Aula Kiadó, Budapest, 300 pp. [in Hungarian]
- KLEIN, D. R. & STRANDGAARD, H. (1972) Factors affecting growth and body size of roe deer. *Journal of Wildlife Management* **36**: 64–79.
- KREYBIG, L. (1937) A Magyar Királyi Földtani Intézet talajfelvételi, vizsgálati és térképezési módszere. [Soil survey, analyses and mapping methodology of the Royal Hungarian Geological Institute.] *Bulletin of the Hungarian Royal Geological Institute* **31**: 148–244. [in Hungarian]
- MIRANDA, B. R. & PORTER, W. F. (2003) Statewide habitat assessment for white-tailed deer in Arkansas using satellite imagery. *Wildlife Society Bulletin* **31**: 715–726.
- MITCHELL, A. (2005) *The ESRI guide to GIS analysis, Volume 2: Spatial measurements and statistics*. ESRI Press, Redlands, CA, 252 pp.
- MYRBERGET, S. (1988) Hunting statistics as indicators of game population size and composition. *Statistical Journal of the United Nations ECE* **5**: 289–301.
- MYSTERUD, A. (2006) The concept of overgrazing and its role in management of large herbivores. *Wildlife Biology* **12**: 129–141.
- MYSTERUD, A., LANGVATN, R., YOCCOZ, N. G. & STENSETH, N. C. (2002) Large-scale habitat variability, delayed density effects and red deer populations in Norway. *Journal of Animal Ecology* **71**: 569–580.
- MYSTERUD, A., MEISINGSET, E., LANGVATN, R., YOCCOZ, N. G. & STENSETH, N. C. (2005) Climate-dependent allocation of resources to secondary sexual traits in red deer. *Oikos* **111**: 245–252.
- MYSTERUD, A., TRYJANOWSKI, P. & PANEK, M. (2006) Selectivity of harvesting differs between local and foreign roe deer hunters: trophy stalkers have the first shot at the right place. *Biology Letters* **2**: 632–635.
- SMITH, C. M., MICHAEL, E. D. & WIANT, H. V. (1975) Size of West Virginia deer as related to soil fertility. *West Virginia Agriculture and Forestry* **6**: 12–13.
- SPSS (2004) *Classification trees™ 13.0*. SPSS Inc., Chicago, IL, 127 pp.
- STREBL, F., GERZABEK, M. H., KARG, V. & TATARUCH, F. (1996) Cs-137-migration in soil and its transfer to roe deer in an Austrian forest stand. *Science of the Total Environment* **181**: 237–247.

- STRICKLAND, B. K. & DEMARAIS, S. (2000) Age and regional differences in antlers and mass of white-tailed deer. *Journal of Wildlife Management* **64**: 903–911.
- STRICKLAND, B. K. & DEMARAIS, S. (2006) Effectiveness of the State Soil Geographic Database (STATSGO) to predict white-tailed deer morphometrics in Mississippi. *Wildlife Society Bulletin* **34**: 1264–1272.
- SWEET, J. C. & WRIGHT, CH. W. (1952) A comparison of weight and antler development between white-tailed deer in Northern and Southern New Jersey. *New Jersey Outdoors* **3**: 3–8.
- SZABOLCS, I. (1966) *A genetikus üzemi talajtérképezés módszerkönyve*. [Methodology handbook of genetic soil mapping in cooperatives.] Országos Mezőgazdasági Minősítő Intézet, Budapest, 351 pp. [in Hungarian]
- TATARUCH, F. & KIERDORF, H. (2003) Mammals as biomonitors. Pp. 737–772. In: MARKERT, B. A., BREURE, A. M. & ZECHMEISTER, H. G. (eds): *Bioindicators and biomonitors – Principles, concepts and applications*. Elsevier, Amsterdam.
- TURNER, M. G., O'NEILL, R. V., GARDNER, R. H. & MILNE, B. T. (1989) Effects of changing spatial scale on the analysis of landscape pattern. *Landscape Ecology* **3**: 153–162.
- VANDEN BRINK, N. (2004) Soil and higher organisms: From bottom-up relations to top-down monitoring. Pp. 215–244. In: DOELMAN, P. & EIJSACKERS, H. J. P. (eds): *Vital soil – function, value and properties*. In: HARTEMINK A. E. & MCBRATNEY, A. B. (eds): *Developments in Soil Science* **29**. Elsevier, Amsterdam.
- VANPÉ, C., GAILLARD, J. M., KJELLANDER, P., MYSTERUD, A., MAGNIEN, P., DELORME, D., VAN LAERE, G., KLEIN, F., LIBERG, O. & HEWISON, A. J. M. (2007) Antler size provides an honest signal of male phenotypic quality in roe deer. *American Naturalist* **169**: 481–493.
- VÁRALLYAY, GY. (1985) Magyarország 1:100 000 méretarányú agrotopográfiai térképe [Hungarian Agrotopography Map at the scale of 1:100 000.] *Agrokémia és Talajtan* **34**: 243–248. [in Hungarian]
- VÁRALLYAY, GY. (1995) Soil data-bases for sustainable land use in Hungary. Pp. 45–68. In: BARTALOS, T., LAL, R. & NÉMETH, T. (eds): *Conservation tillage for sustaining soil and water quality*. AKAPRINT, Budapest.
- VÁRALLYAY, GY., SZŰCS, L., MURÁNYI, A., RAJKAI, K. & ZILAHY, P. (1980) Magyarország termőhelyi adottságait meghatározó talajtani tényezők 1:100 000 méretarányú térképe. II. [Map of soil factors determining the agro-ecological potential of Hungary (1:100 000) II.] *Agrokémia és Talajtan* **29**: 35–76. [in Hungarian with English, German and Russian summaries]
- WAER, N. A. (2001) *Effects of population reduction through increased antlerless harvest on white-tailed deer quality in Alabama*. Thesis (PhD). Auburn University, USA, 56 pp.
- WALTER, W. D., VERCAUTEREN, K. C., CAMPA, H., CLARK, W. R., FISCHER, J. W., HYGSTROM, S. E., MATHEWS, N. E., NIELSEN, C. K., SCHAUBER, E. M., VAN DEELEN, T. R. & WINTERSTEIN, S. R. (2009) Regional assessment on influence of landscape configuration and connectivity on range size of white-tailed deer. *Landscape Ecology* **24**: 1405–1420.
- WHITEHEAD, G. K. (1981) *The game-trophies of the world. International formula for the measurement and evaluation of trophies*. Verlag Paul Parey, Hamburg and Berlin, 215 pp.

Revised version received April 13, 2010, accepted October 21, 2010, published February 28, 2011