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The effects of habitat structure on red deer (*Cervus elaphus*) body mass

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Abstract

In most mammalian species, body mass is one of the key factors affecting an individual's fitness. It is therefore important to know the causes of its variability. The present paper analyses the influences of habitat structure and other environmental factors on body mass in red deer. The research is based on data sets concerning 3,920 culled red deer from the entire Slovenia, which are geo-referenced within a kilometer spatial accuracy, and on 28 spatially explicit raster layers of population density, habitat structure variables (e.g. topography, land use, forest structure, roads) and other environmental variables (e.g. air temperature, precipitation, supplementary feeding). After controlling for sex and age of the individual and its date of culling, body weight significantly differs between population areas, most likely as a result of genotype differences and genotype impact on the phenotype, and is also negatively dependent upon population density and the percentage of conifers and positively dependent upon annual mean air temperature and forest/meadow edge density. The stated environmental factors probably influence the achieved energy balance and, therefore, the body mass of red deer by conditioning the quantity and quality of food and energy expenditure of deer.

Key words: red deer, body weight, habitat structure, environmental factors, population density, forest edge, conifer percentage, temperature, Slovenia

*Vplivi zgradbe habitata na telesno maso jelenjadi (*Cervus elaphus*)*

Izvleček

*Telesna masa je pri večini vrst sesalcev eden najpomembnejših faktorjev, ki vpliva na vitalnost osebka. Zato je pomembno poznati vzroke njene variabilnosti. V raziskavi smo celostno preučili vplive okoljskih dejavnikov na telesno maso jelenjadi (*Cervus elaphus*). Raziskava temelji na podatkih o 3.920 uplenjenih osebkih jelenjadi iz vse Slovenije, ki so georeferencirani s kilometrsko natančnostjo, in na 28 prostorsko-eksplicitnih rastrskih GIS-plasteh, ki podajajo populacijsko gostoto, zgradbo prostora (npr. topografija, raba tal, vegetacija, ceste) ter vrednosti drugih okoljskih spremenljivk (npr. temperatura zraka, padavine, dopolnilno krmljenje). Telesna masa se po kontroliranju vplivov spola in starosti osebka ter datuma njegovega odvzema značilno razlikuje med populacijskimi območji, kar je verjetno posledica vplivov genotipa na fenotip; poleg tega je negativno odvisna od populacijske gostote in deleža iglavcev ter pozitivno od povprečne celoletne temperature zraka in gostote gozdnega roba. Naštete okoljske spremenljivke verjetno vplivajo na doseženo energijsko bilanco in torej tudi na telesno maso jelenjadi s pogojevanjem količine in kakovosti hrane ter porabe energije.*

Ključne besede: *jelenjad, telesna teža, zgradba habitata, okoljski dejavniki, populacijska gostota, gozdni rob, delež iglavcev, temperatura, Slovenija*

1 Introduction

1 Uvod

In most species of large mammals, including ungulates, the relative body weight (i.e. body weight of an animal compared with the body weight of other individuals of the same species, age and sex) is one of the key factors of fitness of an individual because it affects the chances of its survival in the first year of life and its total life expectancy (LOISON / LANVATN / SOLEBERG 1999), age at first reproduction (LANGVATN *et al.* 1996), annual average birth rate (SAND 1996) and reproductive performance over the entire life period (KRUUK *et al.* 1999) as well as the sex structure (CLUTTON-BROCK 1985, WAUTERS *et al.* 1995, KOHLMANN 1999, MYSTERUD *et al.* 2000), body weight and survival probability of its young (KEECH *et al.* 2000). Knowledge on body weight variability and the factors affecting it is therefore relevant in several fields of fundamental ecology (e.g. foraging ecology, ecology of movement and habitat selection), in population dynamics and in wildlife and habitat management.

The paper analyses factors affecting body weight variability in red deer (*Cervus elaphus*), which is considered a key species in forest ecosystems due to its numerous direct and indirect influences on the vegetation

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and soil (see JERINA 2006). Its main purpose is to give complex study of the effects of habitat structure and other environmental factors on red deer body weight.

The majority of previous studies concerning the influences of environmental factors on the body weight in ungulates are based on analyzing long-term variations of the average body weight of animals from the same or different populations with regard to the population density (KLEIN / STRANDGAARD 1972 / CLUTTON-BROCK / ALBON 1983, SAND *et al.* 1996, PETTORELLI *et al.* 2001, PETTORELLI *et al.* 2002) and with regard to density-independent factors, such as year-round weather conditions and cyclic climate oscillations (LOISON / LANGVATN 1998, LOISON / LANVATN / SOLEBERG 1999, POST / STENSETH 1999). Furthermore, some information on effects of topographic variables (MYSTERUD *et al.* 2001) and plant communities on body mass, as well as on population densities and body mass in various habitat types (KLEIN / STRANDEGAARD 1972, JEDRZEJEWSKA *et al.* 1994, PETTORELLI *et al.* 2001, NIELSEN / LINNEL / ANDERSEN 2004) has been gathered for ungulates. Previous research is commonly based on determining the differences in body weight of animals from two or more areas. As the areas compared can differ in several factor layers, such analyses cannot be used to draw definitive conclusions as to what factors actually influence the body weight. In addition, the greater part of previous research has been dedicated to roe deer. The effects of habitat structure on red deer body weight were analyzed only in a few studies carried out in Scotland, Scandinavia and the boreal part of North America, and dealt with one or just a few environmental factors. On the island of Rhum near the western Scottish coast, where red deer inhabits open areas, CONRADT, CLUTTON-BROCK and GUINNESS (1999) analysed the differences in body weight of red deer inhabiting two grassland communities, characterized by different nutritional carrying capacities and preference. In line with expectations, the red deer inhabiting the more preferred community had higher body weight. MYSTERUD *et al.* 2001 studied the effects of topographic variables on red deer body weight in Scandinavia. They discovered that body weight increases with the diversity of altitudes and aspects, and drops with increasing share of high-lying areas and altitude. Due to different environmental conditions, the findings derived from these research projects can hardly be uncritically transposed to the Central-European space, or might be here less relevant. Due to all facts mentioned above, we believe that influences of habitat structure on red deer body weight in Central-Europe have not been yet sufficiently studied.

2 Material and methods

2 Materiali in metode

2.1 Gathering and preparation of data on red deer body weight

2.1 Zbiranje in priprava podatkov o telesni masi jelenjadi

The research is based on data from the Central Slovene Register of Large Game Species and Large Carnivores, which covers the entire Slovenia and contains data on culled large game species and carnivores (described in VIRJENT / JERINA 2004, ADAMIČ / JERINA 2006). For all culled animals the data on their sex, estimated age, body weight, and the cause, date and location of culling are gathered within the Register. For the needs of the Register, the location of culling is determined by using a unified methodology for the entire Slovenia on the basis of kilometre grid maps and corresponding codes; all the data in the Register are geo-referenced to kilometre accuracy. Datasets concerning 4,718 red deer culled in 2004 were collected from the Register, as the latter is currently completed only for the year 2004. In order to prevent potential errors in measuring and subsequent input of data, special attention was paid to data filtering. After the data was matched for logical filters and incomplete data sets were eliminated (described in JERINA 2006), 3,920 data sets were found to be suitable for further analyses as they all contained data on the coordinates of the harvesting site (kilometre accuracy), sex of culled animal, its estimated age (determined from wear of teeth to a year accuracy), date of culling (day) and net body weight (excluding blood and intestines, to a kilogram accuracy). Figure 1 shows that red deer culling sites are clumped in several areas in Slovenia, where the conditions are optimal for the species, whereas other individual sites are dispersed over a large part of Slovenia. Therefore, the collected data are sufficiently representative for Slovenia. Since the data have been gathered in a wide area, highly heterogeneous in structure, they

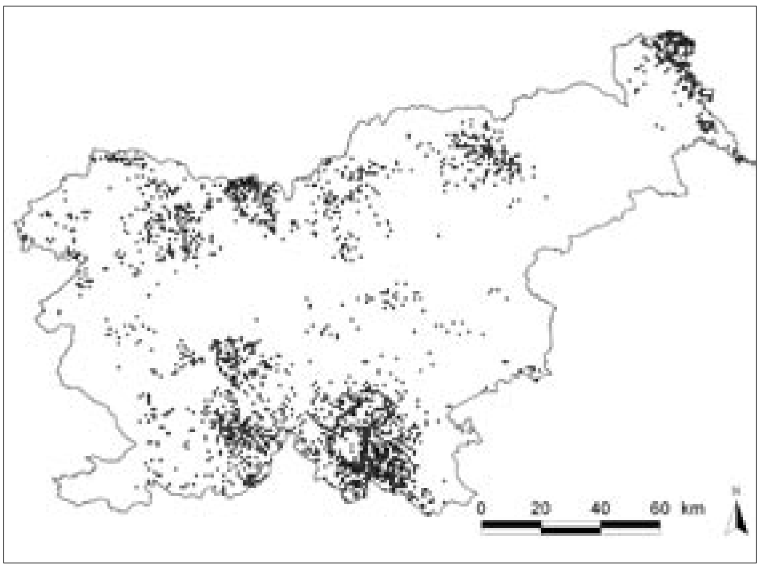

Figure 1: Harvest locations of red deer in Slovenia

Slika 1: *Lokacije odvzema jelenjadi v Sloveniji* cover wide gradients of environmental factors. Therefore it is expected that the effects of the studied environmental variables on red deer body weight should be ascertained, if they only exist.

2.2 Gathering and preparation of data on environmental factors and other data

2.2 Zbiranje in priprava podatkov o okoljskih dejavnikih in drugih podatkov

The research studied influences of numerous variables which, according to the results of Slovenian telemetric analyses of the red deer habitat selection (JERINA 2006), could affect the energy balance of red deer and their body weight by conditioning the quantity of accessible forage and energy consumption. Main results of domestic studies of red deer habitat selection are summarized in next paragraph. When selecting independent variables, we also considered the findings of previous research mentioned in the introduction, which analysed the effects of environmental factors on red deer and other large herbivorous wildlife species body weight.

Telemetric monitoring of a large sample of red deer from several parts of Slovenia (see DEBELJAK *et al.* 2001, JERINA *et al.* 2002, JERINA 2006) shows that the species strongly prefers to inhabit areas that simultaneously offer more food and good security cover: the vicinity of forest edge, early succession stages of forests, young forests, regeneration stands, selection thinning stands and other forest forms with abundant undergrowth; its year-round spatial distribution, especially winter distribution, depends heavily upon supplemental feeding places, as in many areas fodder is the most important nutritional component of red deer winter diet; the species avoids roads and settlements as sources of disturbance. As already mentioned, in Scandinavia red deer body weight has been found to be directly dependent on altitude and the diversity of elevations and aspects. In addition to all the stated variables, the paper also explores the influences of diversity of solar radiation strength and diversity of plant communities, which could affect red deer body weight by conditioning the temperature, food and shelter, and influencing the possibility of selecting the optimum environment.

The studies of body weight variability in ungulates has shown that the body weight is not exclusively affected by habitat structure but also by a number of other factors, in particular the following: (a) age and sex of animal, (b), season, (c) genotype, (d) population density and (d) annual local weather conditions and cyclic climate factors. It is therefore sensible to include these factors in the research and control for their influences, with a view to improving the reliability of the results.

(a) In red deer, increase in body weight with age is sex-specific: males grow faster, their growth phase is longer and final body weight higher than in females (ADAMIČ / KOTAR 1983). Based on the results of previous research (JERINA 2006), the data on female deer were grouped into five and the data on male deer into seven age classes (Table 1). In grouping the data into classes, the frequency of data in each class and differences in body weight between classes were taken into consideration (Table 1).

(b) In the temperate climate areas, red deer body weight varies seasonally, and variations are sex- and age-specific (RIG / LANGVATN 1982, ADAMIČ 1990).

Table 1: Determining the age-class categories of male and female red deer

Preglednica 1: *Določanje starostnih kategorij samcev in samic jelenjadi*

Females (n = 2,123) *Samice (n = 2.123)*				Males (n = 1,797) *Samci (n = 1.797)*			
Age (years) *Starost (leta)*	Category (code) *Kategorija (koda)*	n	Average body mass (kg) *Povprečna telesna masa (kg)*	Age (years) *Starost (leta)*	Category (code) *Kategorija (koda)*	n	Average body mass (kg) *Povprečna telesna masa (kg)*
0–1	0–1 (1)	946	39.8 ± 0.5	0–1	0–1 (6)	727	42.2 ± 0.6
1–2	1–2 (2)	507	55.5 ± 1.0	1–2	1–2 (7)	318	67.1 ± 1.8
2–3	2–3 (3)	216	71.1 ± 1.5	2–3	2–3 (8)	138	99.7 ± 3.8
3–4	3–11 (4)	402	78.6 ± 1.1	3–4	3–4 (9)	131	108.1 ± 3.5
4–5				4–5	4–6 (10)	210	125.4 ± 3.3
5–6				5–6			
6–7				6–7	7–11 (11)	239	140.8 ± 2.9
7–8				7–8			
8–9				8–9			
9–10				9–10			
10–11				10–11			
11–12	over 11 (5) nad 11 (5)	52	76.3 ± 2.8	11–12	over 11 (12) nad 11 (12)	34	134.2 ± 5.0

Seasonal fluctuations in body weight can be described with a second degree polynomial (ADAMIČ / KOTAR 1983) fitted to the specific age/sex category. The dates of culling were assigned ordinal numbers of a hunting year (starting April 1) and quadrated. The age, sex and cull date variables are referred to as primary factors in the continuation of the paper (Table 2).

Table 2: Codes of primary variables

Preglednica 2: *Oznake primarnih spremenljivk*

Variable *Spremenljivka*	Variable code *Oznaka spremenljivke*	Variable type *Vrsta spremenljivke*
Age and gender category *Spolna in starostna kategorija*	SEX_AGE	Categorical variable with 12 categories (see also Table 1) *Kategorialna spremenljivka z 12 kategorijami (glej tudi preglednico 1)*
Date of culling (1 April = 1; 31 March = 365) *Dan odvzema (1. april = 1; 31. marec = 365)*	DAY	Continuous *Zvezna*
	DAY^2	Continuous *Zvezna*

(c) At the end of the 19th century, red deer populations were virtually exterminated from Slovenian territory, but soon afterwards the species was reintroduced in several parts of the country (ADAMIČ 1990). Deer populations, which evolved from various introductions of the species, are genetically different (FRANK 2005), which could be the reason for inter-population variability in body weight because the genotype is a known body weight factor (COULSON *et al.* 1998). With regard to red deer reintroductions and the direction of its spatial distribution, Slovenia was divided into four main population areas: Prekmurje, Pohorje, the Alps and the Karavanke mountain range, and Southern Slovenia (see JERINA 2006 for details).

(d) Research into the effects of population density on the body weight of herbivores states, almost exclusively, a negative correlation between these two parameters (VINCENT *et al.* 1995, DEBELJAK / DŽEROSKI / ADAMIČ 1999, FORCHHAMMER *et al.* 2001). In accordance with these findings and recommendations, the present research analyses two population density indicators, namely mean six-year density of red deer culling within Hunting Clubs, and local culling density in the last year, determined by means of fixed kernel method (WORTON 1989), which uses data from the Central Register of Large Game Species and Large Carnivores (see JERINA 2006a for details).

(e) Body weight of large herbivorous species can be affected by year-round weather conditions and cyclic climate oscillations (LOISON / LANGVATN 1998, LOISON / LANVATN / SOLEBERG 1999, POST / STENSETH 1999). In the present research, two variables describing weather conditions were considered: annual precipitation and air temperature.

For all the stated independent variables except primary factors, raster data layers with 1,000-metre spatial resolution were prepared in the GIS environment, with each raster cell representing the average surface structure below this cell and the neighbouring eight cells. Each cell from all GIS layers thus presents the structure of a plot measuring 3 x 3 kilometres. The size of the basic spatial unit corresponds with the annual home range of red deer in Slovenia (JERINA 2006). In terms of methodology, it would be ideal to know the exact borders of the animal's individual home range for each culled animal, and the values of environmental variables were taken from the animal's home range. As this is not possible, the described method of data gathering was used as closest to the ideal technique.

The values of independent variables were obtained in GIS by covering red deer sites and raster data layers for all red deer individuals. In fact, 3,920 data sets were prepared, including the data on body weight (dependent variable), age class and sex, time of culling (primary factor) and the value of all environmental and other spatially referenced variables for the near surroundings of the site (3 x 3 km) of culling. The list of all independent variables, except for primary factors, their abbreviations and databases from which they were created, are given in Table 3.

2.3 Statistical analyses

2.3 Statistične analize

The effects of independent variables on red deer body weight were analysed with the *general linear model* in *Statistica for Windows 6.0*. The method is multivariate and as such enables us to study main effects and interactions of numeric and attributive independent variables on dependent variable. The following independent variables were explored: (a) primary factors (Table 2), and (b) all other independent variables (Table 3). Since the seasonal dynamics of body weight is age- and sex-specific, the DAY x SEX AGE and the interaction DAY^2 x SEX AGE were included in the model in addition to all main effects. The main effects and interactions of independent variables were included in the model by the use of *forward stepwise* algorithm. Log transformed body weights were used in the model as a dependent variable to meet the assumptions regarding variable variance.

3 Results

3 Rezultati

The results of the analysis are given in Tables 4 and 5. The table shows that the body weight of culled red deer depended largely on the following primary factors: (a) sex and age class of the animal (AGE_SEX), (b) day in the year when the animal was culled (DAY and DAY^2, this variable

Table 3: List, codes and sources of environmental variables

Preglednica 3: *Seznam, šifre in viri okoljskih spremenljivk*

Description of GIS layer *Opis GIS-plasti*	Variable code *Koda spremenljivke*	Unit *Enota*	Data source *Vir podatkov*
Altitude *Nadmorska višina*	ALT_ABS	m	GURS 1995
Altitude range in grid *Razlika med maks. in min. nadmorsko višino v kvadrantu*	ALT_DELTA	m	
Diversity of aspects *Pestrost ekspozicij*	EXP_DIV		
Diversity of solar radiation density *Pestrost jakosti sončnega obsevanja*	SOLAR_DIV		GABROVEC 1996
Average annual temperature *Povprečna letna temperatura*	TEMP	°C	ARSO 2004
Average annual precipitation *Povprečna letna količina padavin*	PERC	mm	ARSO 2004a
Percentage of forests *Delež gozdov*	FOR_%	%	MKGP 2002
Percentage of early succesional stages of forest and of mixed forest-agricultural land *Delež površin v zaraščanju in mešane kmetijsko-gozdne rabe tal*	SUCC_%	%	
Percentage of meadows and cultivated land *Delež travnikov in kmetijskih površin*	MEAD_%	%	
Percentage of other land-use types *Delež drugih oblik rabe tal*	LAND_OTHER_%	%	
Distance to the nearest non-forest *Oddaljenost od najbližjega negozda*	DIST_NON_FOR	m	
Forest edge density *Gostota gozdnega roba*	EDGE	m/km^2	
Percentage of young stands *Delež mladovij*	F_YOUNG_%	%	ZGS 1990, ZGS 2004
Percentage of early and late pole stands *Delež mlajših in starejših drogovnjakov*	F_POLE_%	%	
Percentage of mature stands *Delež debeljakov*	F_MATURE_%	%	
Percentage of stands in regeneration, and selection forests *Delež sestojev v pomlajevanju in prebiralnih gozdov*	F_REGEN_%	%	
Percentage of other forest types (coppice, bushes, litter stands) *Delež drugih oblik gozda (panjevski gozd, grmišča, steljniki, listniki)*	F_OTHER_%	%	
Percentage of conifers *Delež iglavcev*	CONIFER_%	%	
Growing stock *Lesna zaloga*	WOOD	m^3/ha	
Forest association diversity index *Indeks pestrosti gozdnih združb v kvadrantu*	FOR_DIV		
Number of supplemental feeding places in grid *Število krmišč v kvadrantu*	S_FEED_N		ZGS 2004a
Density of provided supplemental feed in grid *Gostota položene krme v kvadrantu*	S_FEED_KG	kg/km^2	
Distance to the nearest supplemental feeding place *Oddaljenost od najbližjega krmišča*	S_FEED_DIST	m	
Distance to the nearest road *Oddaljenost od najbližje ceste*	DIST_ROAD	m	SURS 1997
Distance to the nearest settlement *Oddaljenost od najbližjega naselja*	DIST_SETTLE	m	
Average harvest density of red deer in hunting districts within the past 6 year period *Povprečna gostota odvzema jelenjadi v loviščih lovskih družin v zadnjih 6 letih*	P_DENS_CUM		ZGS 2004b
Local density of harvested red deer estimated on the basis of data from »Core Slovene Register …« – see also JERINA 2006 *Lokalna gostota odvzema jelenjadi, ugotovljena na osnovi podatkov »Osrednjega registra« – glej tudi JERINA 2006*	P_DENS_LOC		Central Slovene Register … Osrednji slovenski register …
Population area (1. Prekmurje, 2. Pohorje, 3. Alps and Karavanke, 4. Southern Slovenia) *Populacijsko območje (1. Prekmurje, 2. Pohorje, 3. Alpe in Karavanke, 4. južna Slovenija)*	POPULATION		

is included in the model as a second-degree polynomial), and (c) the interaction of variables AGE_SEX and DAY. The sum of linear combinations of these three variables and their corresponding multiplicative coefficients generates a function consisting of several sections of concave second-degree polynomials. The function approximates body weight variations of an average red deer during its life (age class) and throughout the year (variables DAY, DAY^2 and interaction AGE SEX and DAY), separately for males and females.

Table 4: Variance components in regression model of red deer body mass

Preglednica 4: *Analiza variance regresijskega modela telesnih mas jelenjadi*

	SS	d.f.	MS	F- value *F- vrednost*	SS (%)
SEX_AGE	667.86	11	60.71	2,072 ***	81.34
DAY	7.61	1	7.61	260 ***	0.93
DAY^2	3.53	1	3.53	121 ***	0.43
SEX_AGE × DAY	6.39	11	0.58	20.0***	0.78
POPULATION	18.17	3	6.06	207 ***	2.21
TEMP	2.84	1	2.84	97 ***	0.35
EDGE	0.50	1	0.50	17 ***	0.06
CONIFER_%	0.51	1	0.51	17 ***	0.06
P_DENS_LOC	3.19	1	3.19	109 ***	0.39
P_DENS_CUM	0.49	1	0.49	17 ***	0.06
Error *Napaka*	110.02	3,887	0.03		13.40
Together *Skupaj*	821.11	3,919			100.00
Intercept *Konstanta*	63,114.40	1	63,114	2154069***	

$R^2 = 0.87$; F (32, 3887) = 758.4***

In addition to primary factors, red deer body weight also depends on the category variable indicative of the population area to which an animal belongs (POPULATION), on both indicators of red deer population density (P_DENS_LOC, P_DENS_CUM) and on the following environmental factors: mean annual air temperature (TEMP), forest edge density (EDGE) and share of conifers (CONIFER_%). The effects of all the stated variables are statistically significant at low risk ($p<0.001$). The described model explains 86.6% of the total body weight variation of red deer in Slovenia; 96.4% of this variation is explained by primary factors, in particular age and sex, over 2% is caused by the population area and less than 2% by other variables, in particular population density and mean annual air temperature.

The above described regression model was used to assess the quantitative change in red deer body weight caused by an increase in the value of the independent variable from its lower to the upper decil. Relative body weight changes are given in index form in the fifth column of Table 5, whereas the absolute changes are presented in the last column of the table. These values refer to red deer with an average body weight of 66.4 kg. In heavier animals, absolute effects of independent variables would be proportionally larger, and vice versa. It is evident from

Table 5: Estimates of influences of environmental factors on red deer body mass

Preglednica 5: *Ocene vplivov okoljskih spremenljivk na telesno maso jelenjadi*

		Parameter estimate *Ocena parametra*	St. error B *St. napaka B*	D_1	D_9	D_9 -D_1 (C)	Exp (B×C)	Estimate of the factor influence (kg) *Ocena vpliva faktorja (kg)*
TEMP		1.61E-02	3.02E-03	5	9	4	1.066	+ 4.4 (3.6 do 5.3)
EDGE		1.00E-05	2.00E-06	746	5263	4517	1.046	+ 3.1 (2.5 do 3.7)
CONIFER_%		-7.00E-04	1.50E-04	15	81	65	0.955	- 3.0 (-3.6 do -2.4)
P_DENS_LOC		-8.00E-05	1.90E-05	25	627	602	0.953	- 3.1 (-3.9 do -2.4)
P_DENS_CUM		-2.20E-04	6.00E-05	10	260	250	0.946	- 3.6 (-4.5 do -2.7)
POPULATION	2-1	-2.88E-02	9.47E-03					
	3-1	-8.49E-02	7.63E-03					
	4-1	-2.90E-02	5.66E-03					
SEX_AGE*								
DAY		2.50E-03	3.18E-04					
DAY^2		-1.00E-05	1.00E-06					
SEX_AGE × DAY*								
Intercept *Konstanta*		4.10E+00	4.49E-02					

LEGEND / *LEGENDA*:
D1 – value of the first decil of variable / *vrednost prvega decila spremenljivke*
D9 – value of the last decil of variable / *vrednost zadnjega decila spremenljivke*
* parameter estimates are not given due to the large number of estimates (see Table 1 and text for explanation)
ocene parametrov niso podane zaradi velikega števila kategorij (glej tudi preglednico 1 in tekst)

the table that if air temperature rises from the lower to the upper decil (from 5 to 9 °C), red deer body weight increases 6.7%, which is 4.4 kg in a deer of average weight. An increase in forest edge density leads to a rise in body weight of 4.6% or 3.1 kg, but an increase in the share of conifers results in body weight dropping by 4.7% or 3 kg. Among all environmental factors considered, red deer population density has the strongest effect on body weight. The model predicts that a simultaneous rise of both density indicators from the lower to the upper decil will result in red deer body weight dropping by approximately 10% or 6.7 kg.

4 Discussion

4 Razprava

Results of the analysis indicate that red deer body weight depends on primary factors, population density, several environmental factors and most likely also on the genotype.

Primary factors, in particular sex and age of an individual, account for the major part of body weight variability. Given that red deer is known as a species with expressed sexual dimorphism, relatively long growth phase and significant seasonal body weight fluctuations, the finding is understandable. The body weight of an adult male deer is 140.8 ± 2.9 kg, almost 80% more than the body weight of an adult female deer, amounting to 78.6 ± 1.1 kg (Table 1); the body weight ratio between adult animals and offspring in their first year is 1 : 2 in females and even 1 : 3.3 in males. Given that primary factors have such a decisive influence on body weight, they need to be considered in studies similar to ours. Otherwise, minor differences in the spatial distribution of both sexes and age classes along the gradient of the studied environmental variable could lead to incorrect findings concerning the effect of this variable on red deer body weight. It needs to be stressed that in red deer, as in other herbivorous wildlife species, the habitat selection of males and females differs and both sexes are spatially segregated for a part of the year (see review in RUCKSTUHL / NEUHAUS 2002).

As expected, significant differences were found in the body weight of animals between population areas. The effects of primary and environmental factors were controlled throughout the analysis. Therefore, the estimated differences in body weight between populations are probably at least partly caused by genetic differences among populations and the effect of the genotype on body weight. The present research cannot conclusively confirm this hypothesis as the effects of environmental factors can be more complex than predicted by the used analytical model. Besides, the recorded differences could also result from an environmental factor not considered in the research. Nevertheless, this is unlikely since the differences between the populations are very high and exceed the magnitude of all the analysed environmental factors. For example, the body weight of red deer from the Goričko area is 21.6% on average, or 14 kg higher than the body weight of red deer in other parts of Slovenia. Moreover, the POPULATION variable explains more body weight variability than all the other environmental factors considered together.

Among other analyzed variables, population density has the greatest influence on body weight. Spatial variations of population density were described using two indicators, namely mean cull density in Hunting Clubs over the period of 6 years and the local cull density in the last year. Both indicators were included in the model as negative values, which means that red deer body weight drops as population density increases. Negative effects of density on body weight have already been observed in several animal species, including red deer. These effects may result from a number of factors, such as reduction of available resources per individual, easier transmission of parasites and diseases and frequent direct negative interactions between individuals (SMITH 2001, KELLEY *et al.* 2005). The impact of these factors may be further increased, as a rise in density normally leads to a reduction of home range size, which has already been observed for red deer in Slovenia (JERINA 2006). The model predicts that the growth in the value of both indicators of the population density from its first to the last decil would result in a loss of 10% body weight of the animal. However, it needs to be stressed that red deer population density rises with the quality of habitats (JERINA 2006). Negative effects of increased densities are therefore partly compensated by the positive effects of higher habitat quality. Consequently, the actual differences in the body weight of red deer among the areas with the highest and lowest population densities are in fact smaller than predicted by the model.

In addition, the results of the multivariate analysis also point to three environmental variables that affect red deer body weight: (a) air temperature and (b) forest edge density have a positive effect, whereas (c) share of conifers shows a negative impact. The directions of variable influences are consistent with the expectations and link previous knowledge on the ecology of nutrition and habitat selection of the red deer with its population dynamics.

(a) Meadows and other non-forest areas are a key feeding habitat of red deer in Slovenia. Grass grazed by red deer constitutes over 30% of the species' year-round diet and over 50% of food consumed in the vegetation period (ADAMIČ 1990). Still, the degree of use of non-forest grazing areas depends heavily upon the availability of the security cover. Telemetric monitoring of red deer in Slovenia has shown that the probability of use of non-forest areas rapidly decreases with increasing distance from forest edges; in monitored animals, only 5% of all locations situated outside the forests were more than 100 m away from the nearest forest edge. The animals left the forest for non-forest areas and returned to the forest in circadian rhythm. Non-forest areas in the vicinity of forest edges increase the total carrying capacity of an area significantly; consequently, the share of these areas or forest edge density has a positive effect on red deer body weight. The analysis of telemetric data of 50 red deer animals in Slovenia has shown that their annual home range size is inversely dependent on forest edge density within the home range (JERINA 2006). This is a further proof that forest edge increases the carrying capacity of an area because red deer in areas with higher forest edge densities need smaller home ranges to satisfy their energy needs.

(b) The share of conifers also affects the carrying capacity of an area. An increase in the share of conifers may result in a reduction of bush and herbal layer due to yearlong light screening. Additionally, an increase in the share of conifers also leads to a reduction in the production of mast seeds (e.g. acorn, beech and oak mast), which are, due to their high energy value, an important and frequent element of autumn and winter diet of red deer (ADAMIČ 1990). Consequently, an increase in the share of conifers reduces the nutritional carrying capacity of the area for red deer, thus affecting the species' body weight. Similar findings were obtained by JEDRZEJEWSKA *et al.* (1994), who studied spatial variations in the density and biomass of five large herbivorous ungulate species in the Bialowieza virgin forest and in the exploitation forests near the Poland-Belarus border. The researchers found that the share of conifers and the share of mature forests explain 71% of biomass variation/ha of the analysed animal species. The authors point out that borealization of forests resulting from formation of pine and spruce monocultures significantly reduces the carrying capacity.

(c) Mean annual air temperature may affect red deer body weight by conditioning the quantity of available food and energy consumption. Air temperature may influence the energy balance of an animal as it conditions the effective temperature of its direct environment and therefore also its consumption of energy required to maintain a constant body temperature (PARKER 1988, PARKER / ROBBINS 1984, PARKER / GILLINGHAM 1990). Besides, a decrease in temperature leads to a drop in ecosystem primary production and shorter vegetation periods (ČREPINŠEK 2002), while also extending the period of snow-cover and the average thickness of snow cover (KASTELEC 2001), both having an important effect on the quantity of food available to red deer and on the consumption of energy required to search for food and for movement in snow (PARKER / ROBBINS / HANLEY 1984, FANCY / WHITE 1985). As a result, lower temperature probably reduces the carrying capacity of an area, while increasing consumption of energy for search of food, movement in snow and maintenance of a constant body temperature.

The mentioned variables affect red deer body weight by conditioning the quantity and quality of the biomass suitable for red deer diet (e.g. non-forest areas, share of conifers, length of vegetation period) and probably also by affecting red deer energy expenditure (e.g. for maintenance of a constant body temperature, movement in snow, etc.), which jointly influence the carrying capacity of an area. In terms of fundamental ecology, the finding is not new. The interaction between the body weight and carrying capacity has been observed in numerous other animal species. Nevertheless, the relevance of the results obtained in this research cannot be ignored, as they explicitly show the environmental variables that influence the body weight of red deer in Slovenia. Since the data has been gathered in the entire territory of the country, which is highly heterogeneous in structure, the results may likely be generalized to a wider area. The data obtained also indicate that, contrary to previous expectations, certain variables such as supplemental feeding intensity and roads, which have a crucial effect on the habitat selection of red deer, do not affect the body weight of the species, which raises new issues and demands explanations. According to the evolution theory, every activity of an organism (including use of space of a certain structure) is sensible only if it enhances the fitness of this organism. Given that body weight is a very good indicator of fitness in ungulates, one could expect that the variables affecting the habitat selection of red deer also affect its body weight.

5 Povzetek

Telesna masa je pri večini skupin sesalcev, vključno s parkljarji, eden ključnih dejavnikov individualne vitalnosti, saj je od nje odvisna verjetnost preživetja osebka, njegova nataliteta in tudi spolna sestava, telesna masa in verjetnost preživetja njegovih potomcev. Zato je poznavanje variabilnosti telesne mase in dejavnikov, ki jo povzročajo, pomembno tako z vidika temeljne biologije kot pri upravljanju živalskih vrst in njihovega okolja. V pričujoči raziskavi smo analizirali, kateri dejavniki vplivajo na telesno maso jelenjadi (*Cervus elaphus*), ki je zaradi več posrednih in neposrednih vplivov na vegetacijo in tla ena ključnih vrst gozdnih ekosistemov v Sloveniji ter je pomembna tudi z ekonomskih vidikov. Glavni namen raziskave je celostno preučiti vplive zgradbe življenjskega prostora in drugih okoljskih spremenljivk na telesno maso jelenjadi.

Raziskava temelji na sistematično zbranih podatkih o telesni masi, spolu, starosti, datumu in lokacijah odvzema 3.920 osebkov jelenjadi iz celotnega populacijskega območja vrste v Sloveniji, ki so geografsko določene s kilometrsko natančnostjo. Za vse lokacije smo v GIS- okolju pripravili podatke o zgradbi prostora (npr. topografija, oblike raba tal, notranja zgradba gozda, oddaljenost od cest in naselij, dopolnilno krmljenje) in drugih okoljskih spremenljivkah (npr. celoletna temperatura zraka, padavine) ter o populacijskih parametrih jelenjadi (npr. populacijska območja, kazalniki populacijskih gostot). Vrednosti spremenljivk smo za vsako lokacijo zajeli iz območja, ki po površini ustreza velikosti celoletnega območja aktivnosti jelenjadi v Sloveniji in obdaja lokacijo. Podatke smo analizirali s posplošenim linearnim regresijskim modelom in za vključevanje spremenljivk v model uporabili algoritem *stepwise forward*.

Regresijski model napoveduje, da na telesno maso najbolj vplivata starost in spol, kar je posledica močno izraženega spolnega dimorfizma in razmeroma dolgega obdobja telesne rasti obravnavane vrste. Povprečna telesna masa doraslih jelenov v Sloveniji npr. znaša 140,8 ± 2,9 kg, kar je za skoraj 80 odstotkov več od telesne mase doraslih košut, ki znaša 78,6 ± 1,1 kg (preglednica 1); pri samicah je razmerje telesnih mas med doraslimi osebki in mladiči v prvem življenjskem letu 1 : 2 in pri samcih celo 1 : 3,3. Glavni učinki in interakcije spremenljivk spol, starost in datum odvzema osebka pojasnjujejo kar 96,6 % skupne pojasnjene variance regresijskega modela telesnih mas.

Skladno s pričakovanji smo ugotovili značilne razlike v telesnih masah med populacijami s 4 obravnavanih območij (Goričko, Pohorje, južna Slovenija, Alpe in Karavanke), ki se med seboj razlikujejo po nastanku in genetskih značilnostih. Populacijska območja pojasnjujejo 2 % od skupne pojasnjene variance modela, kar je več kot vse okoljske spremenljivke skupaj. Med primerjanimi območji se najbolj razlikuje jelenjad v Prekmurju, ki ima v povprečju za prek 20 % večjo telesno maso od jelenjadi v drugih delih Slovenije. Ker smo v modelu kontrolirali vplive okoljskih dejavnikov, so razlike med populacijskimi območji zelo verjetno posledica genotipskih razlik in vplivov genotipa na fenotip.

Na telesno maso značilno vpliva tudi populacijska gostota jelenjadi, kar je verjetno posledica upadanja dostopnih virov na posamezni osebek (predvsem hrane) z naraščanjem populacijske gostote. Z regresijskim modelom smo ocenili, da se ob povečanju obeh kazalnikov gostote jelenjadi iz spodnjega v zgornji decil telesna masa zmanjša za okoli 10 %. Pri tem je treba poudariti, da populacijske gostote praviloma naraščajo s habitatno kakovostjo; to smo evidentirali tudi za jelenjad v Sloveniji. Zato se v naravi negativni učinki povečanih populacijskih gostot delno kompenzirajo s pozitivnimi učinki boljše kakovosti habitata in so dejanske razlike v telesnih masah med območji z največjimi in najmanjšimi populacijskimi gostotami posledično manjše, kot jih napoveduje model.

Analiza kaže, da je telesna masa jelenjadi odvisna tudi od treh okoljskih dejavnikov, in sicer narašča s povečevanjem gostote gozdnega roba in temperature zraka ter upada s povečevanjem deleža iglavcev. Vse tri spremenljivke lahko določajo količino dostopne hrane za jelenjad. Negozdne površine so eden ključnih prehranskih habitatov obravnavane vrste, saj trave sestavljajo prek 30 % njene celoletne prehrane in prek 50 % prehrane v vegetacijski dobi. Vendar jelenjad uporablja le tiste dele negozdnih površin, ki niso daleč stran od gozda. Zato gostota gozdnega roba dobro indicira skupno prehransko nosilno zmogljivost prostora. Z naraščanjem deleža iglavcev v lesni zalogi se zmanjšujejo pokrovnost in biomasa zeliščne in grmovne plasti ter količina mastnih semen drevesnih vrst, kot npr. hrast, bukev, kostanj, ki so energetsko bogat in priljubljen sezonski vir prehrane jelenjadi. Z upadanjem temperature se skrajšujeta vegetacijska doba in primarna produktivnost ekosistemov, hkrati pa se podaljšujeta obdobje s snegom in debelina snega, kar lahko oboje vpliva na zmanjševanje celoletne povprečne količine dostopne hrane. Temperatura zraka lahko vpliva tudi na porabo energije jelenjadi. Temperatura zraka skupaj s hitrostjo vetra in jakostjo sončnega obsevanja namreč določa efektivno temperaturo neposrednega okolja osebka, le-ta pa njegovo porabo energije za termoregulacijo. Poleg tega temperatura zraka vpliva tudi na dolžino obdobja s snegom in debelino snežne odeje in s tem posredno tudi na porabo energije za gibanje in iskanje hrane, ki se z naraščanjem debeline snega skokovito povečuje. Če vplive vseh treh spremenljivk strnemo z vidika energetike jelenjadi, so nanjo vplivale prek določanja količine hrane in porabe energije, kar oboje vpliva na doseženo energetsko bilanco osebka. Na območjih z večjo nosilno zmogljivostjo ima jelenjad večjo telesno maso, in obratno.

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