

## Impact of selective hunting on the trophy size of roe deer: Baltic example

Linás BALČIAUSKAS<sup>1,\*</sup>, Romualdas VARANAUSKAS<sup>2</sup> and Egidijus BUKELSKIS<sup>2</sup>

1. Laboratory of Mammalian Ecology, Nature Research Centre, Akademijos 2, 08412 Vilnius, Lithuania.

2. Department of Zoology, Faculty of Natural Sciences, Vilnius University, M.K. Ciurlionio 21/27, 03101 Vilnius, Lithuania.

\*Corresponding author, L. Balčiauskas, E-mail [linasbal@ekoi.lt](mailto:linasbal@ekoi.lt) / [linas.balciauskas@gmail.com](mailto:linas.balciauskas@gmail.com)

Phone +370 685 34141, Fax +370 5 2729352

Received: 05. October 2015 / Accepted: 14. February 2016 / Available online: 06. June 2016 / Printed: June 2017

**Abstract.** With antlers valued as trophies, ungulates experience high pressures due to selective hunting. The response of the population differs depending on the type of hunting strategy used, and trophies serve as a suitable proxy to answer this question. For example, unrestricted trophy or leisure hunting results in a diminishing quality of trophies. We evaluated the effect of the applied hunting strategy on European roe deer (*Capreolus capreolus*) antler size in Lithuania, Latvia and Estonia between 2006 and 2011. With the aim of preserving good quality bucks up to 5 years of age, compensatory hunting (culling) is obligatory in Lithuania. To the north, in the other two Baltic countries, roe deer buck are hunted with no age limit. Based on nonparametric tests and forward stepwise discriminant function analysis of antler morphometric characters, Lithuanian roe deer antlers were found to be significantly larger (about 40 % by mean weight and volume for the 35 biggest trophies). We conclude that bucks in Latvia and Estonia are hunted out before they reach trophy maturity (5–7 years). The antlers of fast growing bucks in the age of 3–4 years are almost as big, so they are untimely eliminated from the population. We recommend extending the preservation period of healthy roe deer buck to 6 years of age, giving hunters the possibility to estimate their age not solely on antler size, but also on other body characters.

**Key words:** *Capreolus capreolus*, compensatory culling, antler size, Lithuania.

### Introduction

With certain morphologic traits of game selected in most cases, hunting is generally a non-random process (Festa-Bianchet 2003, Johnson et al. 2010). The genetic or population consequences of this however are not always known (Harris et al. 2002, Allendorf & Hard 2009). In most cases, different hunting strategies are employed related to morphological traits of cervids and the age structure in their populations (Martínez et al. 2005). Inevitably, these strategies influence not only the population density, but also the sex and age structure and the genetic mix (Ginsberg & Milnergulland 1994, Harris et al. 2002). Selective hunting of cervids, and in particular roe deer, is common in European countries: selection for better quality trophy (compensatory culling) in Czech Republic, Hungary, Poland, Spain and Germany, while selection for age and gender (calf, hind harvest) – in Finland, France and Norway (see Apollonio et al. 2010).

Though recreational hunting and hunting for meat does not target animals on the basis of size selection (Myserud 2011), trophy hunting is based on the selection of special traits. This selection is influenced by hunting culture and economic or pragmatic interests (Milner et al. 2006). Selection is mainly the preserve of local hunters (Martínez et

al. 2005), and the selection enables commercial hunting to seek trophies of roe deer with bigger antlers (Myserud et al. 2006).

Unlimited trophy hunting exerts a pressure on the populations of game species, tending to act towards a decrease of trophy size. As a result, changes in such morphometric parameters could reflect changes in the local system of hunt management (Rivrud et al. 2013). One of the most expressive examples of this is the reduction in horn size in the rams of bighorn sheep (*Ovis canadensis*), caused by the simultaneous effects of environmental factors and selective hunting based on best trophies (Coltman et al. 2003, Garel et al. 2007, Allendorf & Hard 2009, Hedrick 2011).

Characteristic to Hungary, Germany and Poland for example, an alternative strategy and approach to cervid hunting and trophies is the system of limited trophy hunting as applied through the compensatory hunt (*wahlabschuss* in German) – in this, bucks with shorter and lighter antlers are hunted first (Lockow 1991, Drechsler 1992). The aim of such a style, used in above mentioned countries of Central and Eastern Europe of selection is to preserve the best bucks until maturity (Myserud & Bischof 2010). Selection is based on the presumption that the antler sizes of young and mature individuals are correlated, i.e. young indi-

viduals with good-sized antlers will go on to be mature individuals with good antler sizes (Bowyer et al. 2001, Bartoš et al. 2007, Mills & Peterson 2013). Based on this, the length of the first antlers is a good index of the animal quality (Schmidt et al. 2001). The practice of compensatory hunt is used in Lithuania, but not in Latvia and Estonia (Andersone-Lilley et al. 2010).

In Estonia, licenses for hunting game are issued by the manager of a state hunting district, the tenant of a hunting district or the owner of a private hunting district (Estonia 1994). The user of the hunting district is required to review game trophies and assess medal trophies (Estonia 2002). In Latvia, the maximum permissible quotas are determined each year by the State Forest Service (Latvia 2003). The permitted methods of hunting are the same in all Baltic countries, namely stalking, hunting from hides, calling hunt, driven hunt, search hunt and pursuit of game. However, selection requirements for deer are implemented only in Lithuania (Hunting 2002), as is the requirement to take an exam in order to get permission to hunt adult animals (Medziotojū 2008).

The aim of this study was to show the influence of compensatory roe deer hunting on antler size comparing three Baltic countries with different hunting strategies. In this, we used only measurable traits of antlers from the CIC (Conseil International de la Chasse) trophy evaluation formula (antler weight, length, volume and span), whilst excluding subjective traits used in the scoring of roe deer buck trophies (colour, pearling, coronets and tine ends).

## Materials and methods

### Study area

The three Baltic countries (Fig. 1) were chosen to test the hypothesis that compensatory roe deer hunting leads to an overall increase in antler size. The Baltic states are ideal for this since the system of compensatory hunt for roe deer is not applied at all or used very rarely in Latvia and Estonia (Andersone-Lilley et al. 2010), while compensatory hunting has been used in Lithuania for over 40 years, and has served as the legal basis since 1996.

The three Baltic countries (Estonia, Latvia and Lithuania) are situated in North-eastern part of Europe near the Baltic Sea. Area of the three countries is ca. 175000 km<sup>2</sup>, Lithuania and Latvia being almost equal in size (ca. 64000 and 65000 km<sup>2</sup>, respectively), and Estonia much smaller, ca. 45000 km<sup>2</sup> (Andersone-Lilley et al. 2010). In 2013, forest covered 34.7% of the area of Lithuania, 52.7% of Estonia and 54.0% of Latvia (The World Bank 2016).



Figure 1. Study area in European scale.

### Data collection

Data on roe deer antlers were extracted from the catalogues of hunting trophy exhibitions, specifically in 2009 and 2012 in Lithuania (Lietuvos 2009, 2012), 2013 in Estonia (Eesti 2013) and 2013 in Latvia (Latvijas 2013). From the catalogues, we selected animals hunted in 2006–2011. The trophy measurements were taken by authorized CIC experts and under CIC approved methodology. By the CIC formula, the antler mass without skull is used, thus in cases where antler mass was shown including the skull in the catalogue, 90 g was subtracted (Whitehead 1981). Individuals were aged by use of several traits, namely the wear of teeth in the lower jaw, sutura ossification, as well as size and form of the antler pedicle (Stubbe & Lockow 1994, Baleišis et al. 2003). Gold medals are awarded to roe deer trophies evaluated 130 and more CIC points, silver medal to 115–129.99 CIC points and bronze medal to 105–114.99 CIC points (Whitehead 1981).

In Lithuania, 1029 roe deer trophies were presented to the hunting trophy exhibitions, 390 of which were from animals with known age. Age groups covered were from 3 to 10 years. In our analysis of antler growth tendencies, we used the 390 evaluated trophies with known age of animal. In the hunting catalogue of Latvia there were 63, in the catalogue of Estonia – 66 roe deer trophies though the ages of the individuals were not known.

### Data analysis

To compare the different hunting systems between countries, the 35 biggest trophies from each country were selected (total sample N=105). For further analysis in Lithuania, all trophies from the age groups of 3–4 years and >8 years were analysed, while the 25 biggest antlers were selected in each of the 5, 6 and 7 year-old age groups (the groups containing the most individuals in the sample). The biggest trophies were selected based on CIC points of metric traits, calculated according to the formula

CIC points of metric traits =  $0.3V + 0.1W + 0.5AAL$ , where

V is the volume of the antlers, measured in cm<sup>3</sup>,

W is the dry weight of antlers, measured in g, and

AAL is the mean antler length (sum of the length of the left main beam and length of the right main beam, di-

vided by 2), measured in cm.

In addition, we analysed the span of antlers (despite not being used as a factor in compensatory roe deer hunting in Lithuania), expressed in cm. All measures follow Whitehead (1981).

Index of asymmetry (A) was evaluated according Palmer et al. (1986):

$$A = (R_i - L_i), \text{ where}$$

$R_i$  and  $L_i$  is the length of right and left antler, respectively.

Official game count and bag data for 2006–2009 and 2006–2011, respectively, were used to estimate roe deer population densities (ind./km<sup>2</sup>); we did calculations for the total area and area of the forest in each country.

Normality of data distribution was tested with Kolmogorov-Smirnov test. Nonparametric statistic methods (Kruskal-Wallis rank test, Spearman rank correlation) were used for the analysis of biggest trophies, as data distribution was non-normal (Zar 2010). Right and left antler lengths were compared using Wilcoxon signed-rank test for matched samples, indexes of asymmetry were compared using Kruskal-Wallis rank test. Forward stepwise discriminant function analysis was used to group trophies according antler weight and volume (StatSoft. Inc. 2010).

## Results

### Influence of the hunting strategy on the trophy size (comparison of the three Baltic countries)

Post-hoc analysis showed that parameters characterizing the biggest antler sizes are significantly different between the countries with different strategies of hunting (antler weight  $H = 60.63$ ;  $p < 0.0001$  and volume  $H = 57.0$ ;  $p < 0.0001$ ; length of the main beam, left  $H = 11.10$ ;  $p = 0.0039$ , length of the main beam, right  $H = 16.65$ ;  $p = 0.0002$ , inside span differences are not significant,  $H = 2.50$ ;  $p = 0.2871$ ). In Lithuania, where compensatory roe deer hunting is conducted, the antlers are significantly bigger in all parameters except span. The mean weight of the 35 biggest roe deer antlers in Lithuania was 37.5 % bigger than that in Latvia and 41.3 % bigger than in Estonia; and the maximum weight 15.4 % and 18.4 % respectively. The mean volume of the 35 biggest roe deer antlers in Lithuania was 38.4 % and 38.7 % bigger than in Latvia and Estonia, while the maximum volume was 11.9 % and 6.7 % bigger. Differences in antler length were not so striking (Table 1).

Concerning antler weight, there were outliers in all three countries (much above the mean, Latvia – 557 g, Estonia – 543 g, Lithuania – 643 g; below the mean, Estonia – 234 g.). Outliers for antler volume were observed only in Estonia (254 g) and

Latvia (219, 237 and 242 g), all much above the mean.

There was a strong significant correlation between antler weight and volume in the best trophies in Latvia ( $r = 0.80$ ,  $p < 0.05$ ) and Estonia ( $0.76$ ,  $p < 0.05$ ), but this was weak and not significant in Lithuania ( $r = 0.18$ ,  $p = 0.3$ ). The left and right antler lengths were correlated in all three countries - Lithuania ( $r = 0.77$ ,  $p < 0.05$ ), Latvia and Estonia ( $r = 0.80$ ,  $p < 0.05$ ) - while antler span was not correlated with any other investigated measure in any of the three countries.

Discriminant analysis revealed that groups were separated according to antler weight (Wilks'  $\lambda = 0.329$ ,  $F = 5,080$ ,  $p = 0.0086$ ) and volume ( $\lambda = 0.335$ ,  $F = 6,081$ ,  $p = 0.0032$ ). Two canonical functions separate groups of antlers (Wilks'  $\lambda_{1,2} = 0.298$ ,  $\chi^2 = 121.11$ ,  $df = 10$ ,  $p = 0.0000$ ). Canonical function  $f_1$  explains 97.9 %,  $f_2$  – 2.1 % of dispersion. Roe deer antlers of Lithuanian origin were classified as 100 % correct, while those from Estonia 60.0 % and those from Latvia 57.14 % correct (Fig. 2).

Promising roe deer individuals (hunted in Lithuania at the age of 3–4 years) were not classified so successfully. Groups also were separated according antler weight (Wilks'  $\lambda = 0.357$ ,  $F = 8.903$ ,  $p = 0.0000$ ) and volume ( $\lambda = 0.362$ ,  $F = 9,731$ ,  $p = 0.0000$ ). Two canonical functions separate groups of antlers (Wilks'  $\lambda_{1,2} = 0.296$ ,  $\chi^2 = 157.41$ ,  $df = 6$ ,  $p = 0.0000$ ). Canonical function  $f_1$  explains 95.31 %,  $f_2$  – 4.69 % of dispersion. Second canonical function was also significant (Wilks'  $\lambda_2 = 0.907$ ,  $\chi^2 = 12,544$ ,  $df = 2$ ,  $p = 0.0019$ ). Roe deer antlers of Lithuanian origin were classified 100 % correct, those from Estonia 40.0 % and those from Latvia 37.14 % correct. Classification of promising roe deer antlers was 57.14 % correct.

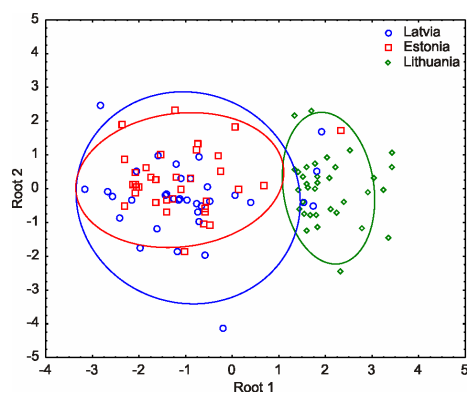
### Symmetry of antlers of roe deer in the Baltic countries

In Latvia and Estonia, significant differences between the lengths of left and right antlers were not found. In Latvia, the values of the differences in the lengths of left and right antlers were distributed not normally (Kolmogorov-Smirnov  $d = 0.194$ ,  $p = 0.002$ ), the mean difference was equal to zero ( $t = 0.34$ , NS) and the mean value of the left and right antler did not differ (Wilcoxon's  $T = 249.0$ ,  $Z = 0.81$ , NS). Thus, there is antisymmetry recorded in the best roe deer antlers in Latvia.

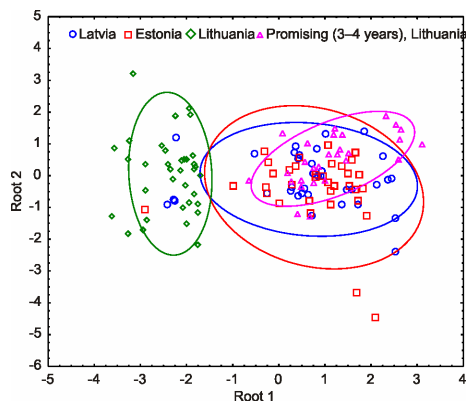
In Estonia, the values of the differences in the lengths of left and right antlers were distributed normally ( $d = 0.139$ ,  $p = 0.084$ ), the mean

**Table 1.** Morphometric characteristics of the biggest roe deer antlers from Lithuania, Latvia and Estonia (N = 35). Roe deer trophies from Lithuania have significantly bigger weight, volume and length. Kruskal-Wallis test multiple comparisons, the same indexes show no significance; a -  $p < 0.0001$ , b -  $p < 0.001$ , c -  $p < 0.01$ .

	Lithuania		Latvia		Estonia	
	Mean (ISE)	Min-Max	Mean (ISE)	Min-Max	Mean (ISE)	Min-Max
Weight, [g]	538.54 (ISE: 38.23) <sup>a</sup>	463.0 - 643.0	391.63 (ISE: 67.43) <sup>b</sup>	256.0 - 557.0	380.97 (ISE: 55.60) <sup>b</sup>	234.0 - 543.0
Volume, [cm <sup>3</sup> ]	231.71 (ISE: 15.99) <sup>a</sup>	205.0 - 271.0	167.40 (ISE: 29.46) <sup>b</sup>	126.0 - 242.0	167.06 (ISE: 22.42) <sup>b</sup>	138.0 - 254.0
Length of main beam, left, [cm]	26.14 (ISE: 1.69) <sup>c</sup>	22.2 - 29.5	24.67 (ISE: 2.05) <sup>b</sup>	20.7 - 29.0	25.07 (ISE: 1.92) <sup>b</sup>	21.1 - 29.0
Length of main beam, right, [cm]	26.59 (ISE: 1.67) <sup>c</sup>	23.2 - 30.9	24.82 (ISE: 1.90) <sup>b</sup>	20.4 - 28.0	24.88 (ISE: 1.89) <sup>b</sup>	21.1 - 28.4
Span, [cm]	11.24 (ISE: 3.5) <sup>b</sup>	5.2 - 21.8	11.07 (ISE: 2.71) <sup>b</sup>	5.7 - 16.2	12.17 (ISE: 3.24) <sup>b</sup>	5.5 - 19.1



**Figure 2.** Discrimination of best roe deer antler trophies from Lithuania, Latvia and Estonia according to first two canonical functions. Analysis indicated significant differences in antlers characters of different hunting strategies (trophies from Lithuania are separated from those in Latvia and Estonia). Elipses represent 95 % confidence levels.



**Figure 3.** Discrimination of best roe deer antlers from Lithuania, Latvia and Estonia and promising roe deer antlers from Lithuania according to first two canonical functions. Analysis indicated significant differences in antler characters of different hunting strategies and age groups (best trophies from Lithuania are separated, while trophies of promising animals from Lithuania are similar to trophies from Latvia and Estonia). Elipses represent 95 % confidence levels.

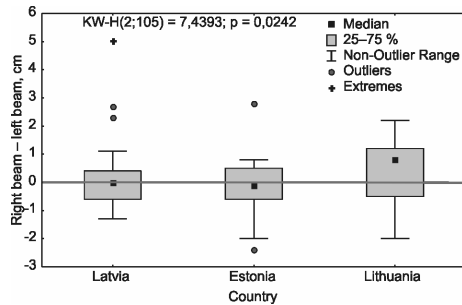
difference was equal to zero ( $t = -1.12$ , NS) and the mean value of the left and right antlers did not differ ( $T = 2289.0$ ,  $Z = 0.94$ , NS). There is fluctuating asymmetry recorded in the best roe deer antlers in Estonia.

By contrast, directional asymmetry was found to exist in Lithuania in the lengths of the roe deer antlers in the best trophies. The values of the differences in the lengths of the left and right antlers were distributed not normally ( $d = 0.169$ ,  $p = 0.012$ ), the mean difference was not equal to zero ( $t = 2.44$ ,  $p < 0.05$ ) and the mean value of the left and right antler differed significantly ( $T = 151.5$ ,  $Z = 2.50$ ,  $p = 0.013$ ). The left antlers were shorter (Fig. 4).

#### Morphometric parameters of roe deer buck of known-age from Lithuania

Analysis of the biggest roe deer antlers in all 3–10 year-old age groups show that between-group differences of antler mass and volume are significant (Kruskal-Wallis,  $H = 78.372$  and  $H = 61.223$  respectively, both  $df = 7$ ,  $p < 0.0000$ ), while differences in antler length ( $H = 11.897$ ,  $df = 7$ ,  $p = 0.1040$ ) and span ( $H = 10.890$ ,  $df = 7$ ,  $p = 0.1435$ ) are not significant. Post hoc analysis of the morphometric antler parameters revealed that 5 to 7 year-old roe deer bucks have the biggest and heaviest antlers, which significantly differ from the antlers of 3–4 and 8–10 year-old bucks (Table 2).

Distribution of the trophy parameters in the



**Figure 4.** Symmetry in the best roe deer trophies from Lithuania, Latvia and Estonia ( $N = 35$  in each country), expressed as the difference between the lengths of right and left antlers. Shorter antlers are symmetric (difference of the length of left and right beams is near zero). Selective hunting enables longer antlers to grow, however, they are asymmetric. Kruskal-Wallis test results are shown by KW-H.

roe deer of known-age from Lithuania show that the increases in antler weight and volume start to decrease after 7 years, while the length and span of antlers are quite stable (i.e. do not depend on the age of animal, Fig. 5). This relationship provides evidence for the further development of selection rules.

## Discussion

In Lithuania, mandatory age estimation and recording was included in trophy evaluation procedures from 2012, thus giving us the possibility to evaluate antler growth tendencies and to find if hunter selection processes help to increase the trophy value in roe deer. However, data on the age of roe deer bucks hunted in Latvia and Estonia are absent, as are the ages of the top Lithuanian roe deer trophies. This is the main limitation of our study, and it is irrevocable, as there are no possibilities to retrospectively evaluate the animal age (the required parts of the skull are missing).

Our analysis proved that differences in antler parameters are significant between the countries with different hunting strategies, and that the biggest trophies are in Lithuania, where compensatory hunting is implemented legally. Selection is conducted by hunting out roe deer bucks characterized by insufficient quality (abnormal antler shape, low body weight (Lockow 1991, Drechsler 1992) and by limiting trophy hunting (Rivrud et al. 2013). In Lithuania, good quality roe deer bucks may be hunted only if they are at least 5 years of

age and have an antler weight of no less than 300–320 g (Baleišis et al. 2003). Hunting of poor condition bucks decreases population and increases trophy quality, conversely than trophy-stalking, when males with good antlers are pursued (Martínez et al. 2005).

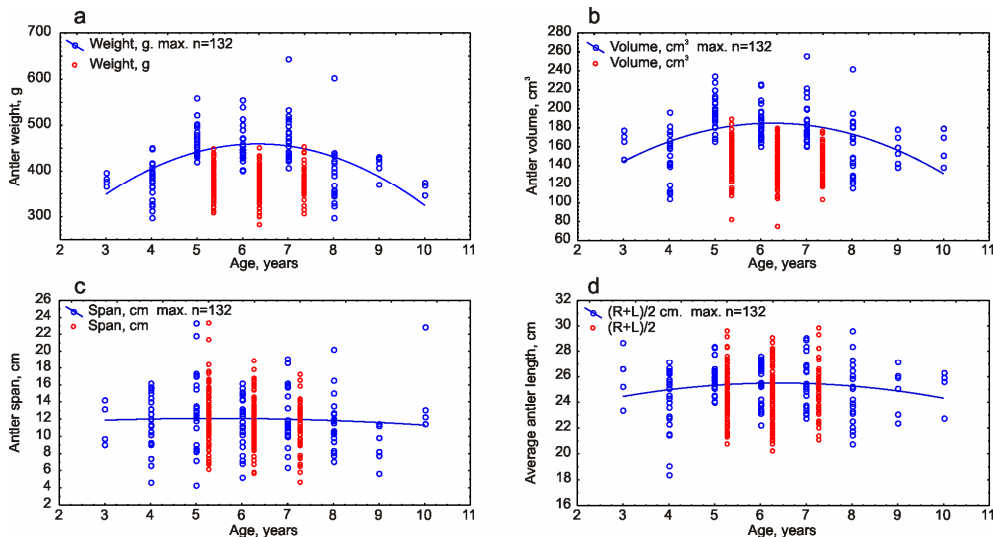
In Latvia and Estonia, roe deer hunting is not strictly regulated (Andersone-Lilley et al. 2010). However, in terms of antler size, the 4 outliers (from  $N=35$ ) in Latvia and 2 outliers (from  $N=35$ ) in Estonia may be characterised as individually performed selection, preserving the best individuals until their full development. These 6 animals in discriminant analysis were classified as of Lithuanian origin (see Fig. 2). As the most important parameters (weight and volume) explain 97.9 % of antler size variation and reliably discriminate between trophies of the different countries, there are two possibilities for these outliers to exist. First, there could be a local selection practice in the hunting club (number of hunted roe deer in the hunting district is sufficient to preserve the best quality animal until full maturity). Second, the roe deer managed to survive themselves – this is considered unlikely however as trophy hunting is popular in both Latvia and Estonia.

We found that antlers of 3–4 year-old roe deer from Lithuania are equal in their parameters to the best antlers from Latvia and Estonia, where compensatory hunting is not used. As fast developing hoofed animals, such as mouflons, may have considerable antler weight at a young age (Garel et al. 2007), it is quite possible that in Latvia and Estonia roe deer bucks are hunted before they reach full trophy development. When young males with promising antlers are preserved, the best trophies are maintained in the population (Strickland et al. 2001). However, trait-specific selection not only changes age structure in the populations. Some authors consider human-controlled selection as a step to semi-domestication of game ungulates (see Mysterud, 2010)

We tried to eliminate other factors affecting antler size in roe deer, thus leaving hunting strategy as the key factor. Correlation between body and antler size is very strong (Stewart et al. 2000, Bowyer et al. 2001, Mills & Peterson 2013). However, antler size is influenced also by several other factors such as environmental pressures, climate and population density (Pélabon & Van Breukelen 1998, Mysterud et al. 2005). Increased population densities (4.7–14.1 ind./km<sup>2</sup>) in roe deer lead to a decrease in mean body mass of yearlings and

**Table 2.** Parameters of the biggest roe deer antlers in animals of known-age from Lithuania (N = 132). Decrease of trophy size is occurring after 7 years of buck age. Asterisk marked values are significantly higher than those not marked, post hoc comparison,  $p < 0.01$ .

		Age, years							
		3	4	5	6	7	8	9	10
Volume, [cm <sup>3</sup> ]	median	168.5	147.5	195	183.5	183.5	148	160	160,5
	Rank	49.5	32.9	101.4	83.8	83.1	42.7	40.4	43,5
	Z	-0.9	-4.76	4.94*	2.45*	2.35*	-3.11	-1.85	-1,22
Weight, [g]	median	381.5	387	455.5	449	466	370	419	359
	Rank	28.5	32.1	94.7	89.4	94.6	37.2	50.4	17,6
	Z	-2.02	-4.87	4*	3.24*	3.98*	-3.82	-1.15	-2,6
N		4	24	24	24	24	21	7	4



**Figure 5.** The distribution of parameters of the biggest roe deer antlers in animals of known age from Lithuania. Circles – biggest antlers in all age groups (N = 132), dots – other antlers with known animal age (N = 258). Curve represents function of antler growth tendencies of biggest antlers. R and L represent of the length of left and right beams, respectively.

subadults and a decrease in antler length in all age subadults and a decrease in antler length in all age classes (Pélabon & Van Breukelen 1998). Quality and amount of available foods, as well as the amount of food per capita decreases not only with increase of population density, it is influenced also by climate and weather conditions (Schmidt et al. 2001). It is known that both year and season influence body mass (Douhard et al. 2013) and antler weight (Bartoš et al. 2007), thus we limited our material to the years 2006–2011 for all three compared countries.

Average roe deer density in 2006–2011 in Lithuania was 1.59 ind./km<sup>2</sup>, that in Latvia 2.93 ind./km<sup>2</sup> and in Estonia 1.38 ind./km<sup>2</sup> ( $H = 8.1135$ ,  $df = 2$ ,  $p < 0.02$ ; however, only two last densities

differ significantly, post hoc,  $p < 0.02$ ). Respective averages of roe deer densities in the forests were 4.80 ind./km<sup>2</sup> in the forested area in Lithuania, 5.64 ind./km<sup>2</sup> in Latvia and 2.82 ind./km<sup>2</sup> in Estonia ( $H = 8.89$ ,  $df = 2$ ,  $p = 0.012$ ; the density in Latvia significantly greater than in Estonia, post hoc,  $p < 0.02$ ). Bag densities, however, did not differ between countries. In Lithuania, on average 0.81 ind./km<sup>2</sup> of forested area were hunted in 2006–2011, 0.64 ind./km<sup>2</sup> in Latvia and 0.55 ind./km<sup>2</sup> in Estonia ( $H = 1.98$ ,  $df = 2$ ,  $p = 0.37$ ). Of note however, even though overpopulation may be another factor that influences antler weight (Kruuk et al. 2002), this can be discounted in our case as roe deer densities in all countries were lower than those shown by Pélabon & Van Breukelen (1998).

According to Radeloff et al. (1999), average densities up to 5 ind./km<sup>2</sup> correspond to poor habitat and are acceptable economically.

In the compensatory hunting strategy, population numbers are regulated by removing the bucks with the worst body condition (Strickland et al. 2001, Festa-Bianchet 2003), thus preserving food sources for animals in better condition (Schmidt et al. 2001). Good quality food is especially essential to roe deer fawns (Pélabon & Van Breukelen 1998). While big antlers are growing, energy consumption is very high (Markusson & Folstad 1997). Bony tissue in the big antlers is more porous (Landete-Castillejos et al. 2012) and the density of the bony tissue is decreased due to deficiency of zinc (Landete-Castillejos et al. 2007).

The geographic aspect of roe deer body weight is not known, so we made some calculations according to data presented by Danilkin et al. (1992). A weak concordance to Bergmann's rule was found, i.e. animal body mass depends on latitude ( $r^2 = 0.23$ ). Although we should expect bigger antlers in northern populations, the reality is vice versa. In other cervids, for example white-tailed deer (*Odocoileus virginianus*), the bigger body size in northern populations is based on better food availability due to lower deer population densities (Wolverton et al. 2009). Food quality and abundance is important for conformance to Bergmann's rule in other ungulates, including moose (*Alces alces*) (Terada et al. 2012). A positive influence of better habitat conditions on antler size is also present in roe deer (Ramanzin & Sturaro 2014). However, given the habitats are approximately equal across the Baltic States (Anderson-Lilley et al. 2010), the lower roe deer densities in Estonia presumably result in a greater food availability. Despite this, antlers are still bigger in Lithuania where the food availability to individual animals is presumably lower. Thus, we propose that hunting selection is the main factor explaining observed trophy differences in the Baltic countries.

#### Baltic aspects of roe deer hunt

It is very important to estimate the age of roe buck up to five years old (Hewison et al. 1999). The most precise age estimation is possible for an animal up to two years old (Cederlund & Kjellander 1991, Mysterud & Østbye 2006), with a precision of ca. 77 % for animals up to four years (Høye 2006). If both tooth wear and pedicle diameter are accounted for, precision is even higher (Mysterud & Østbye 2006). Tooth wear rates are not influ-

enced by habitat quality (Veiberg et al. 2007). Of additional note, the precision of roe deer age estimates are human-biased and depend on the level of experience of the expert (Szabik 1973, Cederlund & Kjellander 1991). Though it is possible that an error of more than one year could have occurred in the age of some bucks older than five years in our study, age estimation in all cases was done by internationally-accredited experts. Thus, we may expect that bias did not overly influence our results.

According to hunting regulations in Lithuania, 5–6 year old roe deer bucks are considered mature and from the 7 year of age as aging. Our analysis show that 5–7 year-old roe deer bucks have no significant differences in antler parameters (see Table 2), thus there is no reason to limit maturity in roe deer to 5–6 year old animals. The only difference between these age categories is the number of hunted individuals.

As a result of our study, we propose three age groups of roe deer bucks according to their antler development: young, physically mature and promising from a hunter's point of view (3–4 years old), mature in the trophy aspect (5–7 years old), and aging (8–10 years old).

Despite limitations in the hunting of young up-and-coming roe deer bucks, some individuals fall having antlers equal in size to those characteristic of mature animals. In the period 2006–2011, 28 promising (3–4 year-old with large antlers) bucks were hunted in Lithuania. They accounted for 7 % of the measured trophies, i.e. significantly less than the number of 5 year-old (33 %,  $\chi^2 = 78.91$ ,  $p < 0.0001$ ) or 6 year-old (32 %,  $\chi^2 = 77.71$ ,  $p < 0.0001$ ) animals. Thus, the main principle of compensatory roe deer hunting in Lithuania (to preserve young up-and-coming bucks and hunt trophies only after the individual is 5 years or older) is justified. The number of large antler trophies significantly decreases from the age of 6 ( $\chi^2 = 13.98$ ,  $p = 0.0002$ ) and declines further with age: 7 years – 20 %, 8 years – 5 %, 9 years – 2 % and 10 years – 1 %. Antlers of 6–10 year-old individuals do not significantly differ in size from the antlers of the young and mature, just the number of trophies from animals of 7–10 years-old is much reduced. The number of young and insufficient quality buck hunted is much higher in Latvia.

Without any doubt, imposed restrictions on the huntable age of individuals bearing large antlers preserve animals until full trophy maturity. This is confirmed by the size of trophies and is in-

fluenced by the hunting strategies employed (Martínez et al. 2005, Mysterud 2011, Crosmary et al. 2013). As a conclusion, the hunter's influence on phenotypic characters is considerable (Allendorf & Hard 2009). Our analysis of roe deer trophies in the three Baltic countries using different hunting strategies for the species fully confirms this (Table 3). The distribution of medals of Lithuanian roe deer was better than that in Latvia and Estonia (both  $\chi^2 = 271.5$ ,  $df = 3$ ,  $p < 0.0001$ ). All biggest Lithuanian roe deer trophies were awarded gold medals. The distribution of medals for Estonian roe deer trophies was significantly worse (less medals awarded) than that of Latvian roe deer (Table 3,  $\chi^2 = 15.8$ ,  $df = 3$ ,  $p < 0.0025$ ).

**Table 3.** Distribution of the number of awarded medals for the biggest roe deer antlers from animals hunted in three Baltic countries, 2006–2011 (35 best trophies from each country).

Country	Gold	Silver	Bronze	No medal
Lithuania	35	0	0	0
Latvia	4	18	5	8
Estonia	4	9	15	7

However, the distribution of medals in the 28 promising bucks sample from Lithuania, not shown in the Table 3 (2006–2011, 1 trophy awarded gold, 12 silver, 7 bronze and 8 antlers undersize for award.) was similar to that in Latvia ( $\chi^2 = 4.01$ ,  $df = 3$ ,  $p = 0.26$ ) and Estonia ( $\chi^2 = 7.65$ ,  $df = 3$ ,  $p = 0.053$ ).

#### Recommendation for implementation

Unnatural selection in populations subjected to hunting affects many biological and population traits. Trophy hunting of antlers may have a population response of reduced antler or body size (Allendorf & Hard 2009). This is not compatible with selection for best trophies, so hunting regulations based on body and/or antler size of the roe deer bucks should apply.

The idea of compensatory hunting, used in Lithuania, is to preserve young up-and-coming roe deer bucks until full maturity and best trophy value (largest antlers). The implementation of compensatory hunting is as follows: hunting of promising young bucks is prohibited, while all individuals are subjected to hunting after the age of 5 years (trophy maturity). Hunters seek to eliminate animals with small and/or abnormal antlers (desirably the first ones) by the beginning of the rut. In this way, population density is also regu-

lated.

Licensing system is strictly implemented for the roe deer bucks (does and juveniles in 2011–2013 were hunted without limits, in 2014 licensing was renewed). With the licenses being of fixed term, some roe buck individuals in full trophy maturity may evade hunting in the allotted season, and thus the quality of trophy can start to decrease by the following season.

However, when trophy hunting is not strictly regulated, young animals with large antlers are selected, excluding their possibility to participate in the breeding process. Smaller individuals with worse trophy values remain and participate in the breeding. In such way we may expect deteriorating of the antler trophies in Lithuania, if hunt intensity of roe deer buck is to be higher in the age 3–4 years.

In contrast, we recommend extending minimum age limit of hunting for roe buck with good quality antlers to 6 years. Based on results of presented study, such change will produce more roe deer antler trophies of the highest value while maintaining population structure favoring older age groups, as recommended by Mysterud (2010). In the same time, ensuring longer presence of the best males in breeding, extended hunting age limit will decrease losses in general genetic diversity in the terms of Harris et al. (2002).

**Conflict of Interest.** The authors declare that they have no conflict of interests.

#### References

- Allendorf, F.W., Hard, J.J. (2009): Human-induced evolution caused by unnatural selection through harvest of wild animals. *Proceedings of the National Academy of Sciences USA* 106: 9987–9994.
- Andersone-Lilley, Z., Balčiauskas, L., Ozolins, J., Randveer, T., Tonisson, J. (2010): Ungulates and their management in the Baltics (Estonia, Latvia and Lithuania). pp 103–128. In: Apollonio M, Andersen R, Putman R (eds.), *European ungulates and their management in the 21st century*. Cambridge University Press.
- Apollonio, M., Andersen, R., Putman, R. (2010): *European ungulates and their management in the 21st Century*. Cambridge University Press.
- Baleišis, R., Bluzma, P., Balčiauskas, L. (2003): [*Ungulates of Lithuania*]. Akstis, Vilnius. [in Lithuanian]
- Bartoš, L., Bahbouh, R., Vach, M. (2007): Repeatability of size and fluctuating asymmetry of antler characteristics in red deer (*Cervus elaphus*) during ontogeny. *Biological Journal of the Linnean Society* 91: 215–226.
- Bowyer, R.T., Stewart, K.M., Kie, J.G., Gasaway, W.C. (2001): Fluctuating asymmetry in antlers of Alaskan moose: size matters. *Journal of Mammalogy* 82: 814.



- Cederlund, G., Kjellander, P., Stålfelt, F. (1991): Age determination of roe deer by tooth wear and cementum layers-tests with known age material. pp. 540-545. In: Transactions of the 20th Congress of the International Union of Game Biologists, Gödöllő, Hungary.
- Coltman, D.W., O'Donoghue, P., Jorgenson, J.T., Hogg, J.T., Strobeck, C., Festa-Bianchet, M. (2003): Undesirable evolutionary consequences of trophy hunting. *Nature* 426: 655-658.
- Crosmary, W.G., Loveridge, A.J., Ndaimani, H., Lebel, S., Booth, V., Côté, S.D., Fritz, H. (2013): Trophy hunting in Africa: long-term trends in antelope horn size. *Animal Conservation* 16: 648-660.
- Danilkin, A.A., Markov, G.G., Stubbe, C., Struchkov, Y. (1992): [Morphometric analysis]. pp.25-43. In: Sokolov V.E. (ed.), European and Siberian roe deer. Nauka Publishers, Moscow. [in Russian]
- Douhard, M., Gaillard, J.-M., Delorme, D., Capron, G., Duncan, P., Klein, F., Bonenfant, C. (2013): Variation in adult body mass of roe deer: early environmental conditions influence early and late body growth of females. *Ecology* 94: 1805-1814.
- Drechsler, H. (1992). On the effectiveness of selective hunting according to antler characteristics for red deer. *Zeitschrift für Jagdwissenschaft* 38: 195-201.
- Eesti Jahimeeste Selts (2013): Jahitrofeede kataloog Jäneda 2013. Jäneda. Available at: <<http://web.ejs.ee/et/uudised-ja-teated/1435-jaenedal-hinnatud-jahitrofeede-kataloog.html>> accessed at: 2016.02.01.
- Estonia: Law on Hunting Management (1994): <[http://faolex.fao.org/cgi-bin/faolex.exe?rec\\_id=005003&database=faolex&search\\_type=link&table=result&lang=eng&ormat\\_name=@ERALL](http://faolex.fao.org/cgi-bin/faolex.exe?rec_id=005003&database=faolex&search_type=link&table=result&lang=eng&ormat_name=@ERALL)>, accessed at: 2016.02.01.
- Estonia: Hunting Act (2002): <[http://faolex.fao.org/cgi-bin/faolex.exe?rec\\_id=080902&database=faolex&search\\_type=link&table=result&lang=eng&format\\_name=@ERALL](http://faolex.fao.org/cgi-bin/faolex.exe?rec_id=080902&database=faolex&search_type=link&table=result&lang=eng&format_name=@ERALL)>, accessed at: 2016.02.01.
- Festa-Bianchet, M. (2003): Exploitative wildlife management as a selective pressure for the life history evolution of large mammals. pp. 191-207. In: Festa-Bianchet, M., Apollonio, M. (eds.), Animal behavior and wildlife conservation. Island Press, Washington, D.C.
- Garel, M., Cugnasse, J.M., Maillard, D., Gaillard, J.M., Hewison, A.J.M., Dubray, D. (2007): Selective harvesting and habitat loss produce long-term life history changes in a mouflon population. *Ecological Applications* 17: 1607-1618.
- Ginsberg, J.R., Milnergulland, E.J. (1994): Sex-biased harvesting and population-dynamics in ungulates - implications for conservation and sustainable use. *Conservation Biology* 8: 157-166.
- Harris, R.B., Wall, W.A., Allendorf, F.W. (2002): Genetic consequences of hunting: what do we know and what should we do? *Wildlife Society Bulletin* 30: 634-643.
- Hedrick, P.W. (2011): Rapid decrease in horn size of bighorn sheep: Environmental decline, inbreeding depression, or evolutionary response to trophy hunting? *Journal of Heredity* 102: 770-781.
- Hewison, A.J.M., Vincent, J.P., Angibault, J.M., Delorme, D., Laere, G.V., Gaillard, J.M. (1999): Tests of estimation of age from tooth wear on roe deer of known age: variation within and among populations. *Canadian Journal of Zoology* 77: 58-67.
- Høye, T.T. (2006): Age determination in roe deer—a new approach to tooth wear evaluated on known age in individuals. *Acta Theriologica* 51: 205-214.
- Johnson, P.J., Kinsky, R., Loveridge, A.J., Macdonald, D.W. (2010): Size, rarity and charisma: Valuing African wildlife trophies. *PLoS ONE* 5: 1-7.
- Kaiser, T.M., Brasch, J., Castell, J.C., Schulz, E., Clausen, M. (2009): Tooth wear in captive wild ruminant species differs from that of free-ranging conspecifics. *Mammalian Biology-Zeitschrift für Säugetierkunde* 74: 425-437.
- Kruuk, L.E.B., Slate, J., Pemberton, J.M., Brotherstone, S., Guinness, F., Clutton-Brock, T., Houle, D. (2002): Antler size in red deer: heritability and selection but no evolution. *Evolution; international journal of organic evolution* 56: 1683-1695.
- Hunting Law of Lithuanian republic (2002): <<https://www.e-tar.lt/portal/lt/legalAct/TARA92E17FDCD13>>, accessed at: 2016.02.01.
- Landete-Castillejos, T., Currey, J.D., Ceacero, F., García, A.J., Gallego, L., Gomez, S. (2012): Does nutrition affect bone porosity and mineral tissue distribution in deer antlers? The relationship between histology, mechanical properties and mineral composition. *Bone* 50: 245-254.
- Landete-Castillejos, T., Garcia, A., Gallego, L. (2007): Body weight, early growth and antler size influence antler bone mineral composition of Iberian Red Deer (*Cervus elaphus hispanicus*). *Bone* 40: 230-235.
- Latvijas Mednieku Asociācijas (2013): Trophy grand prix Riga 2013. Riga.
- Latvia: Hunting Law (2003): <[http://faolex.fao.org/cgi-bin/faolex.exe?rec\\_id=05724&database=faolex&search\\_type=link&table=result&lang=eng&format\\_name=@ERALL](http://faolex.fao.org/cgi-bin/faolex.exe?rec_id=05724&database=faolex&search_type=link&table=result&lang=eng&format_name=@ERALL)>, accessed at: 2016.02.01.
- Lietuvos medžiotojų ir žvejų draugija (2009): Lietuvos medžioklės trofejų parodos katalogas, Panevėžys 2009. Vilnius. <<http://lmzd.lt/files/uploaded/medziokles-trofejai/trofejui-katalogai/2009-katalogas.pdf>> accessed at: 2016.02.01.
- Lietuvos medžiotojų ir žvejų draugija (2012): Lietuvos medžioklės ir žūklės trofejų parodos katalogas, Kaunas 2012: Vilnius. <<http://lmzd.lt/files/uploaded/medziokles-trofejai/trofejui-katalogai/katalogas-trofejui-2012-svetainei-3.pdf>> accessed at: 2016.02.01.
- Lockow, K.W. (1991): Vorhersage der Geweientwicklung des Rothirsches - eine Entscheidungshilfe für Wahlabschuß und Hege. *Zeitschrift für Jagdwissenschaft* 37: 24-34.
- Markusson, E., Folstad, I. (1997): Reindeer antlers: Visual indicators of individual quality? *Oecologia* 110: 501-507.
- Martínez, M., Rodríguez-Vigal, C., Jones, O.R., Coulson, T., San Miguel, A. (2005): Different hunting strategies select for different weights in red deer. *Biology Letters* 1: 353-356.
- Medžiotojų selekcinių kvalifikacijos suteikimo tvarka (2008): <<https://www.e-tar.lt/portal/lt/legalAct/TARA053608065EC>> accessed at: 2016.02.01.
- Mills, K., Peterson, R. (2013): Moose antler morphology and asymmetry on Isle Royale National Park. *Alces* 49: 17-28.
- Milner, J.M., Bonenfant, C., Mysterud, A., Gaillard, J.-M., Csányi, S., Stenseth, N.C. (2006): Temporal and spatial development of red deer harvesting in Europe: Biological and cultural factors. *Journal of Applied Ecology* 43: 721-734.
- Mysterud, A. (2010): Still walking on the wild side? Management actions as steps towards 'semi-domestication' of hunted ungulates. *Journal of Applied Ecology* 47: 920-925.
- Mysterud, A. (2011): Selective harvesting of large mammals: How often does it result in directional selection? *Journal of Applied Ecology* 48: 827-834.
- Mysterud, A., Bischof, R. (2010): Can compensatory culling offset undesirable evolutionary consequences of trophy hunting? *Journal of Animal Ecology* 79: 148-160.
- 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., Østbye, E. (2006): "Comparing Simple Methods for Ageing Roe Deer *Capreolus Capreolus*: Are Any of Them Useful for Management?" *Wildlife Biology* 12: 101-107.
- 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.
- Palmer, A.R., Strobeck, C. (1986): Fluctuating asymmetry: measurement, analysis, patterns. *Annual review of Ecology and Systematics* 17: 391-421.
- Pélabon, C., Van Breukelen, L. (1998): Asymmetry in antler size in roe deer (*Capreolus capreolus*): An index of individual and population conditions. *Oecologia* 116: 1-8.

- Radeloff, V.C., Pidgeon, A.M., Hostert, P. (1999): Habitat and population modelling of roe deer using an interactive geographic information system. *Ecological Modelling* 114: 287-304.
- Ramanzin, M., Sturaro, E. (2014): Habitat quality influences relative antler size and hunters selectivity in roe deer. *European Journal of Wildlife Research* 60: 1-10.
- Rivrud, I.M., Sonkoly, K., Lehoczki, R., Csányi, S., Storvik, G.O., Mysterud, A. (2013): Hunter selection and long-term trend (1881-2008) of red deer trophy sizes in Hungary. *Journal of Applied Ecology* 5: 168-180.
- Schmidt, K.T., Stien, A., Albon, S.D., Guinness, F.E. (2001): Antler length of yearling red deer is determined by population density, weather and early life-history. *Oecologia* 127: 191-197.
- StatSoft. Inc. (2010): *Electronic Statistics Textbook*. Tulsa. OK. StatSoft. <<http://www.statsoft.com/textbook/>>, accessed at: 2015.03.21.
- Stewart, K.M., Bowyer, R.T., Kie, J.G., Gasaway, W.C. (2000): Antler size relative to body mass in moose: tradeoffs associated with reproduction. *Alces* 36: 77-83.
- Strickland, B.K., Demarais, S., Castle, L.E., Lipe, J.W., Lunceford, W.H., Jacobson, H.A., Frels, D., Miller, K.V. (2001): Effects of selective-harvest strategies on white-tailed deer antler size. *Wildlife Society Bulletin* 29: 509-520.
- Stubbe, C., Lockow, K.W. (1994): Alters und Qualitätsbestimmung des erlegten Schalenwildes auf schädelanalytischer und biometrischer Grundlage. Dt. Landwirtschaftsverl, Berlin.
- Szabik, E. (1973): Age estimation of roe-deer from different hunting-grounds of south-eastern Poland. *Acta Theriologica* 18: 223-236.
- Terada, C., Tatsuzawa, S., Saitoh, T. (2012): Ecological correlates and determinants in the geographical variation of deer morphology. *Oecologia* 169: 981-994.
- The World Bank. 2016. <<http://data.worldbank.org/topic/environment>>, accessed at: 2016.02.01.
- Veiberg, V., Mysterud, A., Gaillard, J.M., Delorme, D., Van Laere, G., Klein, F. (2007): Bigger teeth for longer life? Longevity and molar height in two roe deer populations. *Biology Letters* 3: 268-270.
- Whitehead, G.K. (1981): *The game-trophies of the world*. Paul Parey, Hamburg and Berlin.
- Wolverton, S., Huston, M.A., Kennedy, J.H., Cagle, K., Cornelius, J.D. (2009): Conformation to Bergmann's rule in white-tailed deer can be explained by food availability. *The American Midland Naturalist* 162: 403-417.
- Zar, J.H. (2009): *Biostatistical analysis*. 5<sup>th</sup> Edition. Pearson Prentice Hall, Upper Saddle River.
-