

Article

Forest Environmental Conditions Shape Carcass Mass but Not Antler Investment of Red Deer Stags (*Cervus elaphus* L.)—Study from Western European Populations

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Abstract: Population stability depends on environmental conditions and their changes, as well as the availability of energy resources. Animals allocate their energy to maintenance, growth, reproduction, and energy storage; therefore, trade-offs are expected between life history traits. Access to abundant resources is expected to manifest itself in the investment of male individuals in sexually selected traits, such as carcass mass and antler size. The study aimed to analyze environmental climate conditions on the carcass and antler mass, as well as on antler form in red deer (*Cervus elaphus* L.) populations. We analyzed the carcasses and the antler masses and forms of 550 red deer stags from three populations in Central–Western Europe that differ in climate conditions that were hunter-harvested between the 2017 and 2021 hunting seasons. Our data indicated that carcass mass was shaped by the location of the population, stag age, precipitation, and temperature, as well as the number of frost days from January to the harvest date. Antler mass and antler investment depended on stag age but not climatic factors. Regular antler forms were more often observed in the harsh environmental conditions. Our observation confirms that resource trade-off is related to carcass mass of red deer.

Keywords: *Cervus elaphus*; carcass mass; antlers; mass; antler investment; antler form; Central Europe; climatic conditions



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1. Introduction

According to resource allocation theory [1], animals must use energy for various activities, like reproduction or survival [2]. Trade-offs are therefore expected between life history traits [3]. In large herbivores, variations in key resources can result in spatial patterns on both the geographic and intra-population scales [4,5]. Access to abundant resources is expected to manifest itself in the investment of male individuals in sexually selected traits, such as body mass and antler size [5]. Therefore, it can be expected that spatial variations in key resources, as well as their availability during periods of limited availability, may translate into traits such as carcass size or antler weight and form. Antlers are a secondary sexual trait that, apart from in reindeer, characterizes only male cervids. Antler size and weight, like other sexual characteristics, are related to fighting ability, access to females, and position in the dominance hierarchy [6]. Antlers form can be characterized using two measurement system—CIC [7] and Safari Club International (SCI) [8]—that in detail measure different characteristics of the antlers. Measuring the size and quality of red

stag trophies is crucial for hunters, conservationists, and wildlife managers. Moreover, the antler's mass indicates not only the condition of the population, but also the position of a particular individual in the herd. Recent studies have also included analyses of antler form and weight [9,10]; however, they do not cover the impacts of climatic and environmental conditions on carcass and antler mass, as well as antler investment and frequency of antler form.

We used European red deer (*Cervus elaphus* L.) as a model species because it is a typical forest animal of the order Artiodactyla and the family Cervidae, crucial to the functioning of the forest ecosystem. This species is widely distributed in North and South America, North Africa, Asia, Europe, and New Zealand [11–14]. However, they are also observed on agricultural land, such as grasslands that are frequently eaten and damaged. Those areas can provide better forage but also resting zones; therefore, they can improve individual condition [15]. As one of the most important forest species, *Cervus elaphus* L. has been subject to significant impacts from human activities, such as selective hunting, translocations, and habitat fragmentation [16,17], which may have locally resulted in high levels of genetic drift, inbreeding, and the blurring of natural patterns of genetic structure [16]. Phylogeographically, according to mitochondrial DNA sequences there are three genetic lineages of red deer in Europe: (1) the eastern populations from the Balkans and the Romanian Carpathians, reaching north to Austria, Hungary, and the Czech Republic from Sardinia and North Africa; (2) the Sardinian and North African population; and (3) the western population from Iberia and the British Isles to Scandinavia, Germany, and Western Poland [17]. However differences between populations are still discussed [11,18,19].

The red deer populations in Poland vary in density as well as the size of individuals. For instance, the highest densities per 1000 ha of forest area occur in the southwest and north, whereas the lowest is in Central Poland. In addition, historical data have indicated that the weight of red deer in Poland has varied. The lightest deer have been found in Southwestern Poland and the heaviest in the northeastern regions of the country and the Carpathians [10], although the size of individuals has varied both in Europe [17] and in Poland [20]; the causes of this fact are not clear and may depend on several factors. It is assumed that the carcass size of red deer is affected by the interaction of several factors, such as the food availability expressed by the proportion of the broadleaved habitat, stress caused by human activity (including selective hunting), natural selection caused by predators (e.g., wolves), and climatic factors (including snow cover) [10]; however, the effects of climatic conditions on red deer carcass size have not been broadly investigated. Moreover, antler mass can indicate the reproductive success of male individuals, and since antlers are costly to produce, their growth can be affected by environmental conditions [21], but there is little knowledge about the impact of environmental conditions on antler investment and antler form.

We hypothesize that environmental conditions shape body mass and antler size, but can also affect antler investment and regularity of antler form. Taking into account the above criteria, the purpose of our study was to analyze the relationship between carcass mass and antler mass in three different populations of red deer living under conditions of varying access to environmental resources and influenced by different climatic conditions. The present study may help to obtain knowledge regarding the reproduction of this wild species and its relationship with the environment.

2. Materials and Methods

2.1. Analysis of Red Deer Features

We analyzed carcass and antler mass of hunter-harvested red deer (*Cervus elaphus* L.) collected within five hunting seasons (2017–2022) from three locations in Poland (Figure 1). Moreover, the stag hunting season in Poland lasted from the 21st of August to the 28th of February; therefore, only individuals harvested within this period could be analyzed. In Poland, red deer are harvested according to the rules established for the entire country. Stags in their second year of life can be harvested only if their spikes are less than 30 cm; stags in third year (2nd head) with 4 tins on each beam, inclusive; and stags aged 4 and 5 (3rd and 4th head) up to five tins on each beam. In the range of 6–10 year old stags (5th to 9th head); all individuals without the crown can be harvested. The oldest stags, from 11 years old (10th head), can be harvested regardless of the form of antlers. In the case of does, it is recommended to harvest individuals with the weakest condition first. Moreover, according to the Polish legal rules of stag hunting and harvesting, only the following stags can be harvested: stags from 1 to 5 years old without the presence of a crown on antlers; between 5 and 10 years old, only stags with the presence of a crown on only one antler, but always individuals characterized by below-average antler and carcass quality from the populations. These restrictions are not obligatory when older individuals are harvested. However, although such regulations apply throughout Poland and have not changed during the harvest period, it can be assumed that all data obtained are influenced by the selection rules applicable at a given time, allowing them to be compared and treated as random data. No animals were killed specifically for the study.

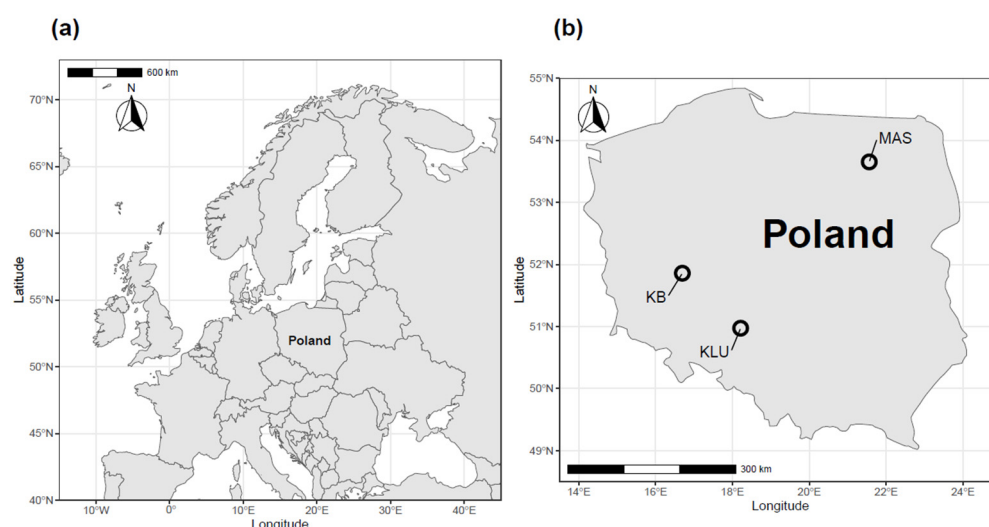


Figure 1. Locations of harvested populations in Europe (a) and in Poland (b). Abbreviations indicate analyzed populations: MAS—Maskulińskie; KB—Karcza Borowa; KLU—Kluczbork.

The number of hunted stags in each location depended on the population size and structure connected to the total forest area. However, the following data have been collected for each individual: region of harvesting, the date of the harvest, stags age, carcass mass (kg), antler mass (kg), and the form of the antlers (number of tines).

To determine the age of the animals, the dentition features and the degrees of their clashes were analyzed [9]. The red deer stags were divided into five classes: 1st class—stags 2 years old; 2nd class—stags 3–5 years old; 3rd class—stags 6–8 years old; 4th class—stags 9–11 years old; and 5th class—12 years and older. All red deer individuals younger than 2 years were excluded from the analysis.

To determine body mass, we used stag carcass mass (± 1 kg) that was measured without head and antlers, whereas antler mass (± 0.01 kg) was measured with skull without mandible. We used a ratio of antler mass over body mass, which, according to Mattioli [5], can quantify antler investment in terms of efforts to build conspicuous secondary sexual traits.

Antler forms were classified into regular (R) and non-regular (NR) forms (Figure 2). The regular form indicated antlers with the same number of tines on each branch [22]. Non-regular forms indicated a higher number of tines on one branch. The forms of the antlers were classified as follows: none (n), spike (SP), 6R, 6NR, 8R, 8NR, 10R, 10NR, 12R, 12NR, 14R, 14NR, 16R, 16NR, 18R, 18NR, 20NR, 22NR, fork (F), and bizarre (B). The number of tines on less developed branches was not determined, and such antlers were classified as non-regular.

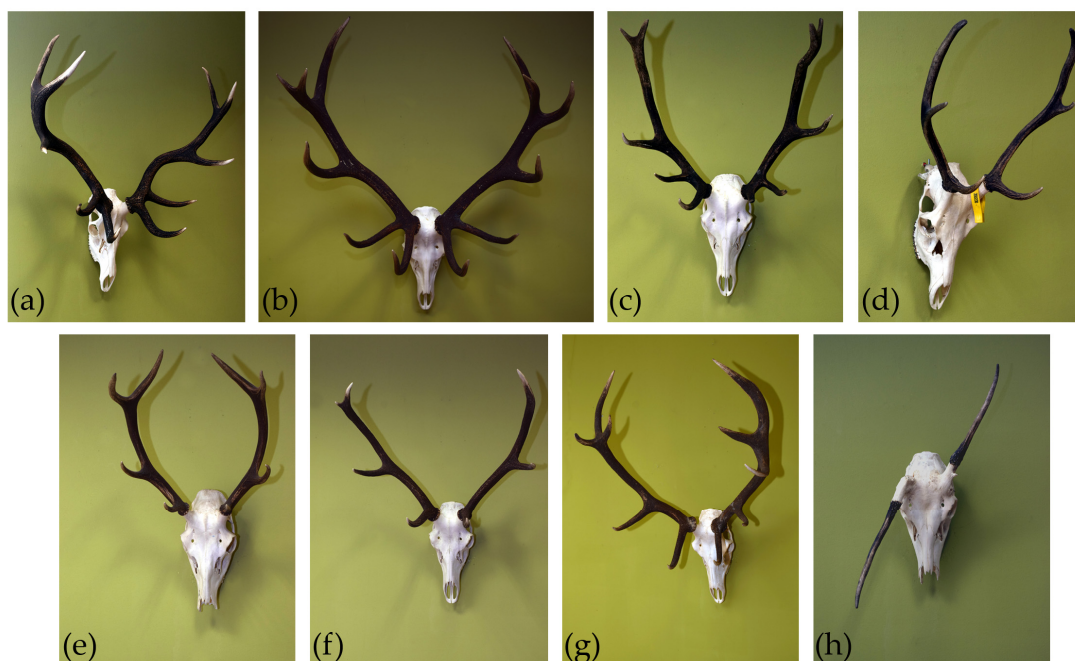


Figure 2. Different forms of antlers: (a) stag with antler form 10 R; (b) stag with antler form 12 R; (c) stag with antler form 10 NR; (d) stag with antler form 6 R; (e) stag with antler form 8 R; (f) stag with antler form 8 NR; (g) stag with antler form 10 R; and (h) spike with broken pedicle. R—regular, NR—non-regular antler form.

Therefore, for each harvested individual, the following data were collected: day of harvest, location, carcass and antler mass, and type of antler form.

2.2. Study Sites

Studies were conducted in three different forest districts—Karczma Borowa, Kluczbork, and Maskulińskie—which represent varied climatic (e.g., temperature, precipitation, snow cover) and habitat conditions (forest type) (Table 1).

We classified the forests as follows:

1. Karczma Borowa (KB)—Central–Western Poland. The climate of this region is transitional between oceanic and continental, and milder than in the eastern parts of Poland [23];
2. Kluczbork (KLU)—mild weather conditions prevail in these areas, especially in the western part (located on the Oder River). This location has the longest growing season in Poland and very favorable amounts of precipitation, especially for agriculture [24];

3. Maskulińskie (MAS)—the climate is harsher here than in other locations; the presence of large lakes leads to high precipitation (677 mm) and relative humidity (80%) [25].

Table 1. Characteristics of the forest of Red Deer (*Cervus elaphus* L.) populations [23–25].

Parameter	Location of Population		
	KB	KLU	MAS
Geographical coordinates	51°84′–51°42′ N 16°23′–16°56′ E	50°51′–51°10′ N 17°54′–18°27′ E	53°47′–53°50′ N 21°33′–21°48′ E
Total area (ha)	12,698.24	19,032.07	28,329.85
Forest area (ha)	12,211.61	18,484.85	26,065.35
Percentage of broadleaved forests (%)	48.9	61.3	10.0
Vegetation period (days)	210	220	200–205
Mean forest age (years)	58	60	83
Grazing forest plots (ha)	9.0	36.8	31.0
The density of red deer per 1000 ha	21	33	20
Optimal density of red deer per 1000 ha	25–30	25–30	25–30

2.3. Climatic Data Collection

We assumed that resource allocation including antler building by red deer stags could be affected by main climatic factors, as severe climatic conditions may interfere with the ability of individuals to store carcass reserves, creating a trade-off between growth, survival, and subsequent reproduction [26].

Among selecting climate factors, we focused on the factors during which antler growth and development occur, as well as changes in individual red deer stag condition before and after the deer mating period.

Each month within the hunting season was characterized by mean monthly precipitation (mm/month), monthly average daily temperatures (°C), and the mean number of frost days (days with temperatures below zero) as the main climatic factors affecting populations to determine resource allocation. These climatic characteristics were calculated from January to the harvest date for carcass mass analysis from the last hunting season.

We downloaded a dataset from the Climatic Research Unit (University of East Anglia) and Met Office (CRU TS Version 4.06 database [27]). The climatic data for the red deer populations were obtained from the database using the ‘raster’ package [28].

2.4. Statistical Analysis

We started the analysis by using all predictors and using the Akaike Information Criterion (AIC) to choose the most parsimonious model to analyze overdispersion. We used population location as a random factor (1 | location), whereas precipitation, temperature, and the number of frost days (January–harvest date) were fixed factors. We used the lmer4 package for mixed models [29]. Results were treated as significant when $p < 0.05$. Maps were provided using the ‘ggmap’, ‘sf’, and ‘ggspatial’ packages. Plots were produced based on the ggplot package. Statistical analyses were conducted using R 4.2.2 software [30]; available online: 21 June 2023).

We performed ANOVA followed by Tukey test to describe the effect of localization of population on analyzed features of carcass and antlers mass and antler investment. We also used the chi-square test to compare the frequency of age classes of hunted stags and the frequency of antler forms between populations. Data were presented as mean values with standard deviation (SD). Data were described as statistically significant when $p < 0.05$.

3. Results

In five hunting seasons (2017–2021), 550 red deer stags were hunted between late August and February, and they were hunted as follows: 343 stags in the KLU Forest District, 118 stags in the MAS, and 89 stags in the KB Forest District. The total number of hunted stags varied over the years (2017: 123; 2018: 95; 2019: 141; 2020: 140; 2021: 51) and differs over the months (in total: September: 170; October: 46; November: 95; December: 77; January: 117; February: 45).

The proportion of stags from different age classes differed between populations and ranged as follows: in the 1st class (none in KB), from 0.29% in KLU to 2.54% in MAS; in the 2nd class, from 14.61% in KB to 38.14% in MAS; in the 3rd class, from 35.59% in MAS to 45.77% in KLU; in the 4th class, from 18.95% in KLU to 32.58% in KB; and in the 5th class, from 0.29% in KLU to 8.99% in KB ($\chi^2(2, 550) = 46.8032, p < 0.001$) (Figure 3, Table A1).

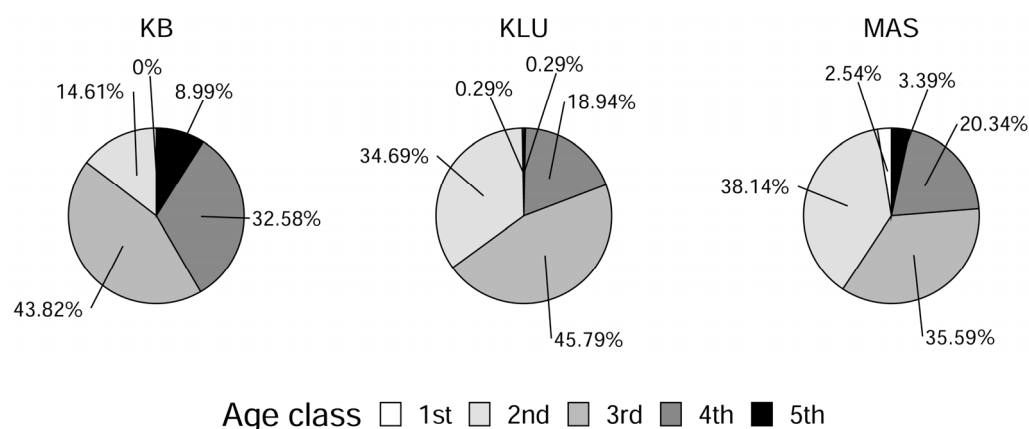


Figure 3. Proportion of different age classes of Red Deer stags harvested by hunters in three populations in Poland between 2017–2021. KB—Karczma Borowa Forest; KLU—Kluczbork Forest and MAS—Maskulinskie Forest.

Carcass mass was shaped by the location of the population, stag age, mean precipitation, mean temperature, and mean number of frost days from January to the harvest date ($AIC = 4592.06$, $R^2_m = 0.364$, $R^2_c = 0.588$, Table 2). Stags from KB had the highest mean carcass mass and differed from other populations (Table 2).

Table 2. Predictors for carcass and antler mass, and antler investment of red deer (*Cervus elaphus* L.) stags of three populations in Poland in 2017–2021. CI—confidence interval, p —probability.

Predictor	Carcass Mass			Antler Mass			Antler Investment		
	Estimate	CI	p	Estimate	CI	p	Estimate	CI	p
(Intercept)	−135.39	−197.69–−73.08	<0.001	−0.58	−4.30–3.15	0.760	1.48	−2.76–5.72	0.494
Stag age	3.54	3.00–4.08	<0.001	0.53	0.50–0.57	<0.001	0.34	0.31–0.36	<0.001
Minimal temperature	21.33	16.01–26.66	<0.001	−0.32	−0.94–0.30	0.313	−0.02	−0.38–0.35	0.3968
Mean temperature	−	−	−	0.31	−0.09–0.70	0.132	−	−	−
Frost days	9.45	6.19–12.71	<0.001	0.01	−0.21–0.23	0.953	0.05	−0.14–0.24	0.610
Precipitation	0.45	0.28–0.62	<0.001	−	−	−	0.00	−0.02–0.01	0.368
Random effects: $n = 3$		$R^2_m = 0.364$ $R^2_c = 0.588$			$R^2_m = 0.556$ $R^2_c = 0.741$			$R^2_m = 0.546$ $R^2_c = 0.650$	

The mean carcass mass varied over the months. The highest carcass mass in the pooled data was noted in September (136.1 ± 12.0 kg), and the lowest in February (98.6 ± 16.9 kg); however, these values differed between the locations. The reduction reached 28.23% in KLU (from September to February), 26.65% in KB (from September to January), and 22.2% in MAS (from October to February) (Figure 4a). The reductions in carcass mass during

autumn and winter differed between populations. It was also revealed that the changes in carcass mass varied between stag age classes. The reduction in carcass mass was the lowest in the 4th class (16.52%), whereas the highest was in the 5th class (27.2%). The carcass mass increases also differed between the populations. Our data revealed higher carcass mass increases from the 2nd to 5th age classes in KLU (+40.0%, from 96 to 135 kg), while the lowest increase was in KB (16.5%, from 127 to 147 kg) (Figure 4b).

Antler mass ($AIC = 1564.7$, $R^2_m = 0.556$, $R^2_c = 0.741$), as well as antler investment ($AIC = 1223.7$, $R^2_m = 0.546$, $R^2_c = 0.650$), were affected by stag age (Table 2). The lowest mean values were recorded in KLU, and the highest mean values in KB (Table 3). The increases in antler mass from the 2nd to 5th age classes differed between the populations. The lowest increase was recorded in KLU (+107%); it was slightly higher in KB (+120%), and the highest in MAS (+125%) (Figure 4c).

Table 3. Mean values of carcass and antler mass, and antler to carcass mass ratio of red deer (*Cervus elaphus* L.) stags of three populations in Poland in 2017–2021. Data were presented as mean and standard deviation. Values with different letters indicate statistically significant differences between populations from different locations.

Parameter	Locations			<i>p</i>
	Karczma Borowa	Kluczbork	Maskulinskie	
Mean carcass mass (kg)	138.7 ± 21.1 a	112.8 ± 20.2 b	112.1 ± 20.8 b	0.001
Mean antler mass (kg)	6.39 ± 1.95 a	3.71 ± 1.47 b	4.04 ± 1.95 b	0.001
Antler investment (%)	4.59 ± 1.17 a	3.22 ± 0.97 b	3.49 ± 1.37 b	0.001

The antlers of the analyzed stags were classified into 20 types of antler forms. Antler forms characterized as SP, F, and B were observed in 5.27% of stags (29/550; 3, 2, and 24, respectively), whereas 44.9% (247/550) of stags possessed a regular form of antlers, while 49.82% (274/550) of them had a non-regular form of antlers. In total, from all 20 types of antler forms the most frequently observed were 12 NR (15.2%), 10 R (13.8%), and 10 NR (13.4%). Two of them were also frequently observed within populations; however, their participation differs between populations. According to share of antler forms, the three most frequent forms in KB were 14 NR (22.47%), 10 R (15.73%), and both 12 N (11.24%) and 12 NR (11.24%); 10 NR (18.08%), 12 NR (17.49%), and 10 R (13.12%) in KLU; and 8 R (16.10%), 10 R (14.41%), and 12 NR (11.86%) in MAS (Table A1).

When only stags with R and NR antler forms were considered, the highest frequency of stags with R form was observed in MAS (60.36%, 67/111), compared to KB (42.86%, 36/84) and KLU (44.17%, 144/326) (χ^2 (2, $n = 521$) = 9.5395, $p < 0.01$). We observed that stags with NR antler forms had higher antler mass (4.54 kg) compared to regular form counterparts (3.92 kg; $p < 0.0001$), and these was statistically significant for two populations: KB and KLU; however, similar trend was observed in MAS (Table 4). Moreover, there were no significant differences in mean carcass mass between R and NR stags ($p > 0.05$); however, populations differed between each other. NR stags were characterized by statistically significant higher index of antler investment in KB and KLU, but not in MAS (Table 4).

According to climatic conditions, we have recorded higher mean monthly precipitation in KLU (29.8–89.1 mm) during the whole year, which exceeded the values recorded from KB (25.2–75.6 mm) and MAS (25.5–74.8 mm). The precipitation in KB and MAS reached similar values during the year. The mean monthly temperature was the lowest in MAS (−3.64–+19.78) during the whole year. Temperature was similar between KB (−0.7–+20.9) and KLU (−0.9–+20.1). Similarly, the number of days with frost during the year was higher in MAS (up to 117 days in a year) when compared to KLU (106 days) and KB (up to 96 days) (Figure 5a–c).

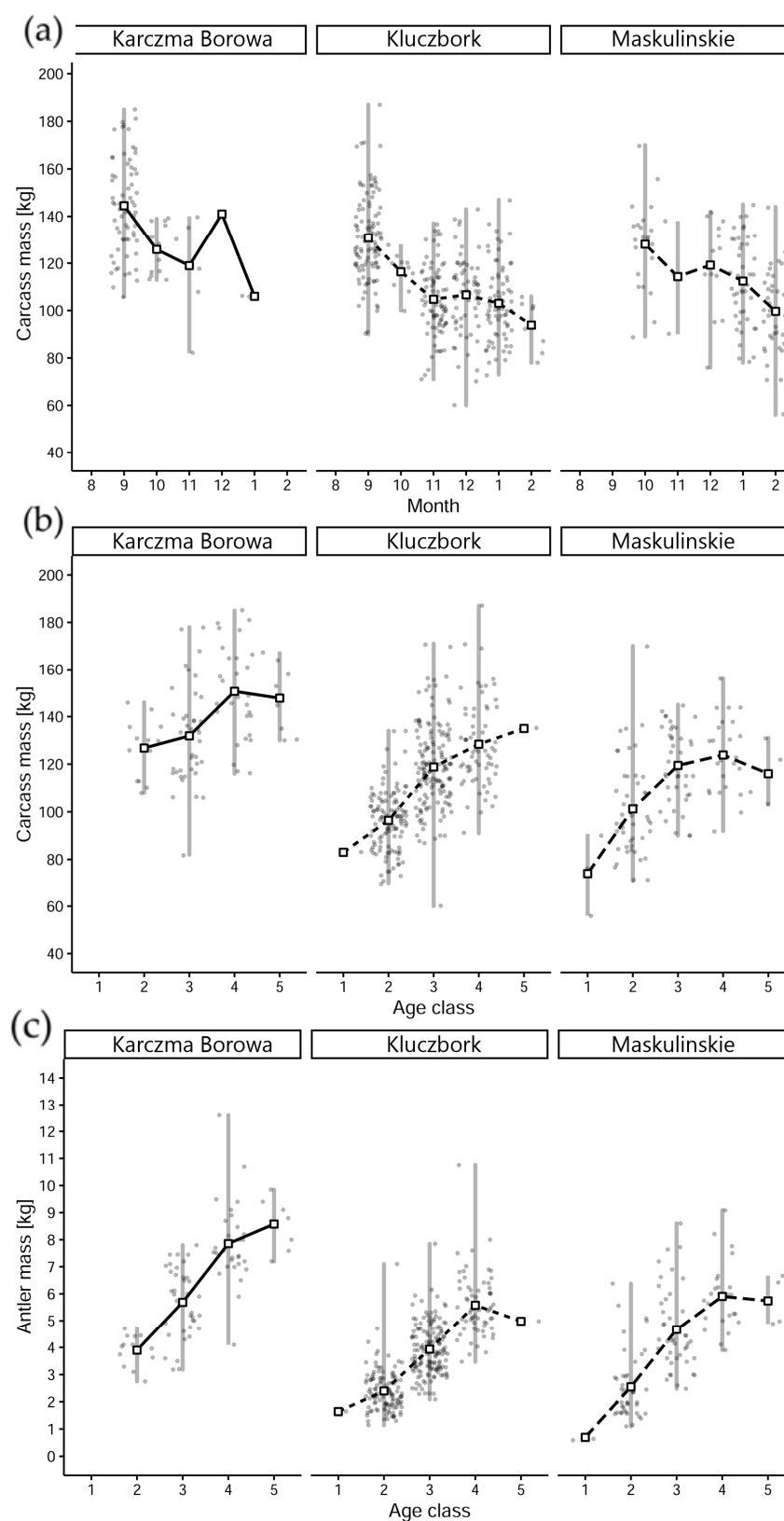


Figure 4. Mean carcass mass (kg) within (a) months, mean carcass mass (b) as well as mean antler mass (kg) (c) in age classes of red deer (*Cervus elaphus* L.) stags of three populations in Poland in 2017–2021 (August–February). The points represent the data for individual stag, the vertical lines represent the range of the value, and the white square indicates the mean value of each month or age class.

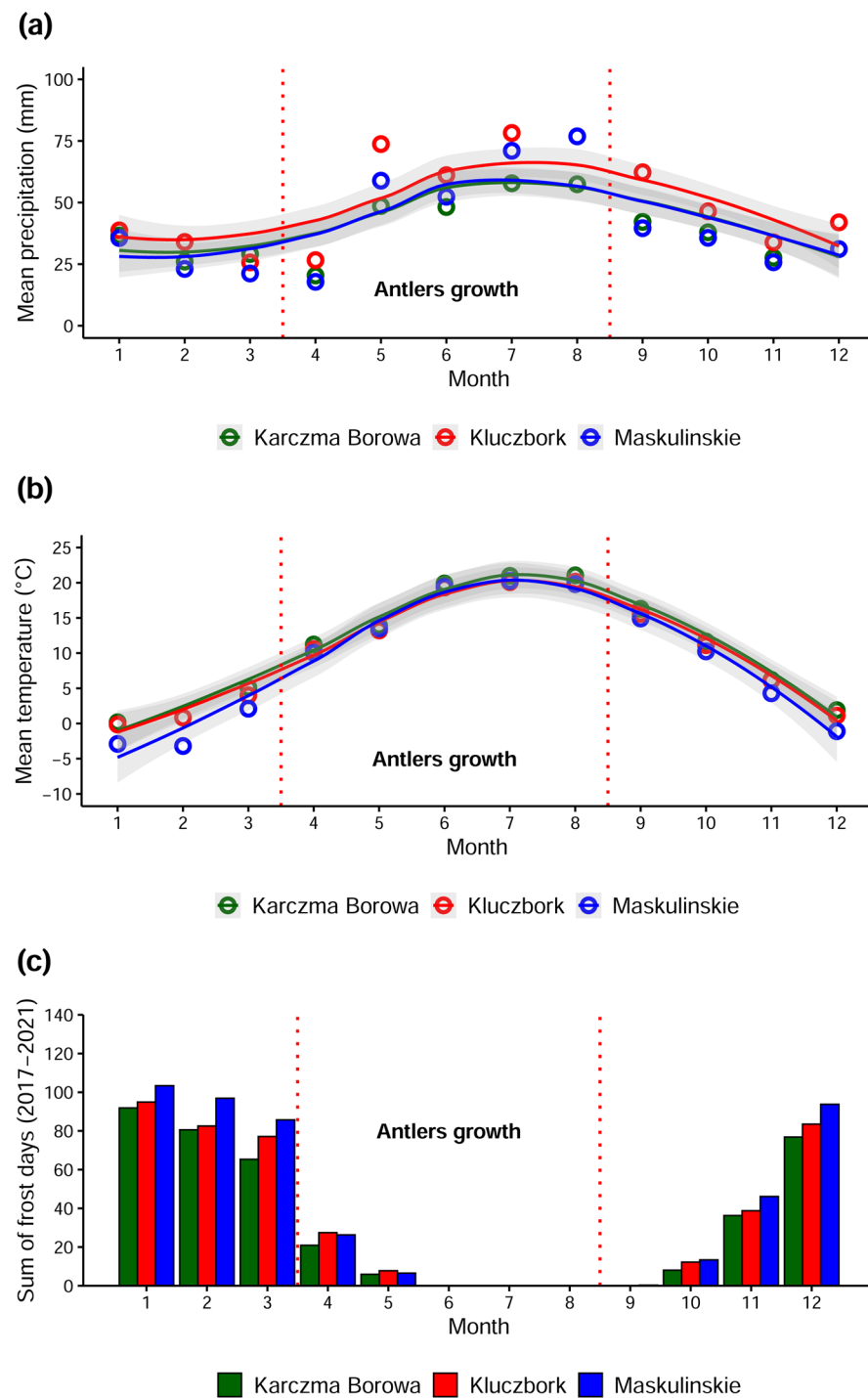


Figure 5. Characteristics of mean environmental conditions of three populations of red deer in 2017–2021 described by (a) mean precipitation (mm), (b) mean temperature (°C), and (c) sum of frost days.

Table 4. Mean values of carcass and antler mass, as well as antler investment of red deer (*Cervus elaphus* L.) stags of three populations in Poland in 2017–2021 in relation to antler form (R—regular and NR—non-regular). Data were presented as mean and standard deviation. Values with different letters indicate statistically significant differences between populations from different locations (a,b) and groups with different antler’s form (x,y).

Parameter		Locations			<i>p</i>
		Karczma Borowa	Kluczbork	Maskulinskie	
Mean carcass mass (kg)	R	134.05 ± 22.38 a	110.84 ± 21.55 b	110.34 ± 21.93 b	<0.001
	NR	139.67 ± 18.94 a	115.05 ± 18.97 b	117.21 ± 16.79 b	<0.001
	<i>p</i>	0.218	0.062	0.081	
Mean antler mass (kg)	R	5.68 ± 1.79 ya	3.51 ± 1.45 yb	3.84 ± 2.00 b	<0.001
	NR	6.78 ± 1.93 xa	3.96 ± 1.46 xb	4.50 ± 1.64 b	<0.001
	<i>p</i>	0.009	0.007	0.069	
Antler investment (%)	R	4.21 ± 1.03 ya	3.09 ± 0.91 yb	3.35 ± 1.42 b	<0.001
	NR	4.85 ± 1.25 xa	3.40 ± 1.00 xb	3.79 ± 1.14 b	<0.001
	<i>p</i>	0.0145	0.0046	0.089	

4. Discussion

The reproductive success of red deer stags depends on its success in defending harems or mating territories, as red deer is a highly polygynous species [31]. Therefore, sexual selection can promote the evolution of secondary sexual traits, such as body and antler mass, thus a stag’s dominance is largely determined by both traits. However, sexually selected traits are costly and can be better afforded by individuals living in better conditions or with better resource availability [32]. Our data indicates that environmental conditions such as precipitation, mean temperature, and mean number of frost days affect mean carcass mass, but not mean antler mass or antler investment. In our studies, those two features were affected by stag age. Moreover, we observed that mean antler mass, as well as antler investment, were higher in stags characterized by the presence of non-regular antler form compared to regular counterparts. Regular antler form was more frequently observed in populations characterized by a greater scale of environmental stress. Furthermore, stags from harsh conditions lose carcass mass more slowly during autumn and winter time, compared to their counterparts.

Our observation pointed out that the highest stag carcass mass (over 138 kg on average) was recorded in the population in Karczma Borowa, which is located in the southwestern part of Poland, which is characterized by higher mean monthly temperature but also the lowest number of days with frost during the year. Therefore, costs related to thermoregulation were lower compared to red deer living in Maskulinskie, where the highest number of frost days as well as the lowest mean monthly temperature were observed together with lower carcass mass. Our data are in line with others [9,33–35]. Carcass and antler mass vary between population localization, which may be caused by habitat conditions, the genetic characteristics of individual populations, varying population densities and climatic conditions, among other factors [9]. Our data indicate that carcass mass is shaped by climatic conditions, such as precipitation and temperature (minimal and maximal), but those environmental factors had no effect on antler mass and antler investment. Analyzed climatic factors, through their influence on plant phenology [36], shape the quality and digestibility of food. For instance, delayed lignification resulting from a cool onset of vegetation (May–June) leads to longer access to high-quality forage and, consequently, greater weights [36,37].

As an example, a positive relationship between temperature and calf mass has been shown in red deer populations in Highland [38]. A similar relationship has been shown by Borkowski [38] in calves in the Raciborskie Forests. Our results are also consistent with those of previous reports on stag carcass mass in Poland [20,39–41]. Interestingly,

the carcass mass of the stags from the population in Kluczbork was about 10% higher than the results reported from the areas of Wielkopolska [34] and Opole [9], which may suggest a slight recent increase in the carcass mass of harvested stags. We also revealed varying increases in stag carcass mass among the age classes. The highest total increase in stag carcass mass from the youngest to the oldest individuals was observed in the population in Kluczbork (a cumulative increase of 40%), and the lowest was observed in the population in Karczma Borowa (of 17%). In addition, the rates of weight increase varied based on age class and were the highest in individuals representing younger age classes. These higher increases are consistent with a study by Czyżyk et al. [42], who reported that carcass mass can increase by as much as 25% between 2 and 3 years and then more slowly in older age classes. In our study, the highest stag carcass mass was recorded in the population in Kluczbork (on average, about 139 kg), which is similar to the results obtained by Bobek et al. [33] in the area of Southeastern Poland, where bull carcass mass has ranged from 108 to 148 kg [41]. In addition, Wajdzik [9] has reported an average stag carcass mass of about 110 kg in the Opole area; this is lower than our results for the nearest population in Kluczbork. Therefore, a new question arose: When did the full physical development of the red deer stags occur in the populations studied? The answer is between the ages of 9 and 11 (the 4th age class in our study), which has been confirmed by the data from Karczma Borowa and Maskulińskie. Our results have also revealed the smallest range of mass variation in older individuals, i.e., over 12 years of age in the populations from Karczma Borowa and Maskulińskie. According to Zalewski and Szczepanski [43], in populations in Northeastern Poland, the full physical development of red deer stags occurs between 6 and 7 years of age. Our study indicated a loss of carcass mass during the post-horn period in all populations studied. The lowest mass loss occurred in the Maskulińskie population (a decrease of about 22.6%) and the highest in the Kluczbork (a decrease of about 27.8%) within a winter period. The results obtained are consistent with those presented by Nasiadka et al. [10], who reported a range of carcass mass loss between 20 and 35% over that period. The observed pronounced decrease in the carcass mass of stags is a result of the high energy costs of the rigor they underwent.

Beside the importance of climatic conditions, the carcass mass may be also shaped by the forage and food, which is connected with the forest habitat type. It has been also proved that the proportional abundance of broadleaved forest in the total cover area is crucial for the condition of individual red deer [9]. In our forests, the total forest area ranges from ~12 to ~28 thousands of ha, which means that we had large forest areas where abundant populations may occur. Further, the proportional abundance of broadleaved forest was highest in Kluczbork (~60%) and Karczma Borowa (~50%) and lowest in Maskulińskie (~10%) forests. Previous studies of Wajdzik et al. [9] proved that less afforested areas (forest area < 40%) with higher proportion of fields were characterized by higher red deer carcass mass in all age classes when compared to stags living in forest areas (forest area > 40%). Similar observation was also done by Mysterud et al. [15]. Our studies were conducted in typical forest areas (forest area > 40%); therefore, among environmental factors, only the proportional abundance of broadleaved species may be important. Moreover, all analyzed populations had similar densities. Earlier start of the growing season has an impact on sooner access to high-quality forage, which affects the condition of individuals (carcass mass) and can manifest itself in better antler quality. In our study, the growing season was similar between locations and ranged from 200 to 210 days. This difference may be crucial in the case of particularly harsh winter conditions (when it is difficult for animals to access food for a longer period of time), which could manifest itself in lower carcass mass in the population from Maskulińskie. The observed effect of environmental conditions on the increase in carcass mass of stags may reflect selection related to access to does and thus

to reproduction success and the transmission and maintenance of the genetic pool in the population [44].

We observed that antler mass depends on stag age but is not affected by environmental conditions such as temperature or precipitation. The effect of stag age on antler development, including antler mass, has been repeatedly documented by other researchers [42,43,45]. We observed that the average antler mass of the stags in Karczma Borowa was higher in each age class compared with those in the other populations. On the other hand, the highest increase in antler mass occurred at up to 9 to 11 years of age (age class 4), which is consistent with the results presented by Łabudzki [34] from the Greater Poland area and Zalewski [46] from the Warmia and Mazury areas. Our results revealed the largest antler mass to be in Karczma Borowa (8.60–9.40 kg) in 11- to 13-year-old stags. In other populations, we obtained lower values, i.e., in Kluczbork (5.8–6.3 kg) for ages 10 and 11, and in Maskulińskie (6.3–6.7 kg) for ages 11–15. Our results are in line with those of Zalewski [46], who noted the culmination of antler mass at 6.3 kg at 9–12 years of age in the Warmia and Mazury regions. On the other hand, Łabudzki [34] showed climaxes that occurred at 11 (5.13 kg) and 12 (5.04 kg) years of age. Similar results from the Pisz Forest area were obtained by Żurkowski [47], who noted that antler mass climaxed at the age of 7–10 years and obtained values from 4.1 to 4.7 kg. The highest antler mass was for stags at age 11 (5.6 kg). Similar correlations were recorded for the population in Bory Tucholskie, where the highest average antler mass (5.9 kg) was recorded for stags aged 11 and older [48]. The development of antler mass in all the presented populations did not differ from the results presented by other authors.

Antler mass of stags was age-related, but not related to climatic factors. Both antler mass, as well as antler investment, were stag age dependent. Red deer from Karczma Borowa had heavier antlers, and antler investment reached higher values than other populations. However, Karczma Borowa and Kluczbork were characterized by lower frequency (~40%) of regular antler form compared to Maskulinskie, where more than 60% of all harvested stags had R antler form. Red deer that had NR antler forms were characterized by higher index of antler development and higher antler mass, which can be connected to fluctuating asymmetry theory. According to that theory, in stress conditions, red deer stags could invest resources into production of regular, symmetrical antler form that further underlines the importance of antler shape in reproductive success [49]. Moreover, cost related to secondary sexual traits, e.g., antler development, can be modulated not only by production cost, but also by benefits resulting from their presence. Antler size is also dependent on the level of intra-sexual competition; thus, red deer males living in female groups produced smaller antlers compared to red deer living in male groups [50]. It was also observed that, each year, approximately 6% of red deer are injured in a fight [51]. Therefore, higher antler mass as well as better quality, described by antler investment and symmetrical form, could be quantitative markers of stag condition. We observed that, in harsh conditions, red deer had lower carcass mass and antler mass, and although antler investment was decreased, red deer more often had symmetrical antler form. On the other hand, red deer living in better environmental conditions with potentially more available resources and lower cost of thermoregulation had higher carcass mass, antler mass, and antler investment, but more often individuals produced non-regular antler form. Thus, sexually selected traits are expected to represent the quality of the individual bearing them [52], and more symmetrical antler form results in lower probability of antler damage during fighting [53], as well as possibly higher reproductive success; therefore, red deer living in harsh environmental conditions can be described by better individual condition compared to individuals living in better conditions. Further, red deer living in better environmental conditions with higher resource availability can invest more in antler mass;

thus, it can compensate for the presence of non-regular antler form. Moreover, as others have pointed out, antler building (antler investment) depends on age but is also affected by food availability, red deer density, and climate [5,54–56]. In our study, density of red deer population was highest in Kluczbork, but not in Karczma Borowa where we observed the highest antler mass. Mateos et al. [49] found that environmental variability is less important in individuals at the prime age. The development of antlers is a product of individual potential, functional needs, and the availability of building substances, which mainly come from food intake. The availability of agricultural land determines increased carcass mass [57], as well as carcass and antler mass [9]. In Southwestern Poland, stags with higher antler mass were recorded, which is consistent with the results obtained from the Kluczbork area in our study. Similar relationships have been reported in populations in northern Italy, in areas characterized by large areas of agricultural land [5]. These relationships can be explained by increased environmental diversity [33] and a long ecotone that fills the needs of this species [9,58,59]. However, our outcomes similar to other studies conducted on wild animals, could also undergo hunter-selection pressure.

5. Conclusions

Environmental conditions shape individuals' features related to secondary sexual traits. Our data indicated that individual quality of red deer stags described by carcass mass is controlled by environmental factors (precipitation, mean minimal temperature, and number of days with frost), but those factors had no impact on antler mass and antler investment. Moreover, harsh environmental conditions can promote the presence of regular antler form, and these can also be controlled by genetic selection or adaptation. Our observation confirms that resource trade-off is related to secondary sexual traits of red deer.

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Institutional Review Board Statement: Approval from the ethical committee for animal experiments is required in Poland for studies or experimentation on animals. According to Article 2, point 2, subpoint 1 of the Act of 15 January 2015, on the protection of animals used for scientific or educational purposes (<https://dziennikustaw.gov.pl/D2015000026601.pdf>, accessed on 7 November 2024), we did not study animals. Our research involved post mortem examination of bones (jaw) of red deer (*Cervus elaphus* L.) hunted by hunters under the Hunting Law (<https://isap.sejm.gov.pl/isap.nsf/download.xsp/WDU20230001082/T/D20231082L.pdf>, accessed on 7 September 2024) and the Regulation of the Minister of Climate and Environment on the list of game species (<https://isap.sejm.gov.pl/isap.nsf/download.xsp/WDU20050450433/O/D20050433.pdf>, accessed on 7 November 2024).

Data Availability Statement: Data is contained within the article. The original contributions presented in the study are included in the article, further inquiries can be directed to the corresponding author.

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Appendix A

All data were presented within the manuscript.

Table A1. Numbers of Red Deer classified according to different forms of antlers within different age classes that were hunted-harvested in three populations—Karczma Borowa (KB), Kluczbork (KLU), Maskulińskie (MAS)—in the years 2017–2021. Each number represents the maximum times for all beams. NR—irregular form; R—regular form, SP—spike form; F—fork, B—bizarre form.

Antler Form	KB					KLU						MAS						Total	
	2nd	3rd	4th	5th	Total	1st	2nd	3rd	4th	5th	Total	1st	2nd	3rd	4th	5th	Total		
SP	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	3	3
F	-	-	-	-	-	-	2	-	-	-	2	-	-	-	-	-	-	-	2
6NR	-	-	-	-	-	-	2	-	-	-	2	-	-	-	-	-	-	-	2
6R	-	-	-	-	-	-	33	1	-	-	34	-	11	-	-	-	-	11	45
8NR	3	-	-	-	3	-	35	5	1	-	41	-	4	2	-	-	-	6	50
8R	2	3	-	-	5	-	20	22	1	-	43	-	14	5	-	-	-	19	67
10NR	1	3	-	-	4	-	9	48	4	-	62	-	6	2	-	-	-	8	73
10R	5	8	1	-	14	-	5	32	7	1	45	-	8	7	2	-	-	17	76
12NR	-	8	2	-	10	-	3	36	21	-	60	-	1	8	4	1	-	14	84
12R	1	6	3	-	10	-	1	4	8	-	13	-	-	7	1	-	-	8	31
14NR	1	6	9	4	20	-	1	2	6	-	9	-	1	3	7	1	-	12	41
14R	-	1	3	1	5	-	-	1	8	-	9	-	-	3	5	2	-	10	24
16NR	-	1	3	-	4	-	-	-	7	-	7	-	-	1	-	-	-	1	12
16R	-	-	-	1	1	-	-	-	-	-	-	-	-	1	-	-	-	1	2
18NR	-	-	1	2	3	-	-	-	1	-	1	-	-	-	1	-	-	1	5
18R	-	-	1	-	1	-	-	-	-	-	-	-	-	1	-	-	-	1	2
20NR	-	1	2	-	3	-	-	-	1	-	1	-	-	-	-	1	-	1	5
22NR	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	1
24NR	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1
B	-	2	3	-	5	1	8	6	-	-	15	-	-	2	2	-	-	4	24
Total	13	39	29	8	89	1	119	157	65	1	343	3	45	42	24	4	118	550	

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