

ANATOLIY VOLOKH, Melitopol / Ukraine

Investigation of Red Deer (*Cervus elaphus*) antlers in the Ukrainian Steppe and results

Key words: antler, area, hybridization, hunting, mammals, management, population, red deer, steppe zone, trophy, Ukraine

Introduction

In response to dwindling populations of red deer (*Cervus elaphus* Linnaeus, 1758), intra-species hybridization became widely used in the late nineteenth century to produce offspring from crosses of different subspecies. Most often used for this purpose were the Siberian red deer (*Cervus elaphus sibiricus* Severtzov, 1873), the Caspian red deer or Maral (*Cervus elaphus maral* Ogilby, 1840) and the Wapiti (*Cervus elaphus canadensis* Erxleben, 1777). According to photographs from 1896–1905, a hybrid derived from crossbreeding of the Central European red deer (*Cervus elaphus hippelaphus* Erxleben, 1777) and the Wapiti inhabited the forests near Upper Schleswig (Germany), the antlers of which contained 22 tines and in length exceeded 1,2 m. To secure these valuable characteristics among other German deer, this specimen was even given the nickname «Hubert» and no hunter was given the right to take him (MEERWARTH, 1909).

Significant hybridization results were also achieved in the Askania-Nova reserve, where from 1902–1950 West European and Siberian red deer were first crossed and then their hybrids: with Siberian, Caspian and Crimean (*Cervus elaphus brauneri* Charlemagne, 1920)

red deer, Manchurian Wapiti (*Cervus elaphus xanthophygius* Milne-Edwards, 1867) and Wapiti (TREUS, 1968). The result was a breed of deer named the Askanian Steppe Maral (Fig. 1). It is well known that hybridization occurs more readily in the genus *Cervus* than in other genera of deer, with a consequence of increased heterozygosity and reproductive potential (HARRINGTON, 1985). Of course, according to modern conceptions of biodiversity conservation, the creation of hybrid breeds and their subsequent resettlement in nature is not considered desirable because it distorts naturally occurring geno-



Fig. 1 Askanian red deer (Azov-Syvash National Nature Park, Biriuchy Peninsula: 01.17.2009) (Photo by A. Volokh)

types and has a significant influence on heredity. However, such organisms can be valuable for cultivation in the agricultural sector, as evidenced by humanity's successes in selectively breeding various domestic animals. Moreover, there are known to be specimens at the borders of different red deer subspecies' ranges of which are likely to have a hybrid origin. Thus, in places where populations of *Cervus elaphus sibiricus* and *Cervus elaphus xanthopygus* intersect, the unique subspecies *C. wachei* Noack and *C. biedermanni* Matschi (MATSCHI, 1907), have been described, which cannot be found anywhere else. It is therefore not surprising that in countries with well-developed hunting cultures, such as Austria-Hungary, Great Britain, Germany and others, there have been many attempts to create hybrids for the purpose of improving the trophy qualities of the deer. In the late nineteenth century elk were important into the territory of Czech lands, which

then mixed with local animals (MEERWARTH, 1909). Consequently, free hybridization of deer in Askania-Nova was welcomed, as it was widely practiced at that time in many countries. Given that in the early twentieth century not a single species of ungulates has lived in the steppe zone of Ukraine, credit is due to F. von Falz-Fein, founder of the Askania-Nova reserve and his followers, for the work in the creation of unique varieties of deer. That said, it should be noted that they did not intend to breed this animal for the population of hunting grounds. This purpose occurred to Soviet functionaries later, with the result that 415 red deer were introduced into the regions of Donetsk, Zaporizhia, Luhansk, Mykolaiv, Odessa and Kherson from 1918–2010, 220 (53,0 %) of which had Askanian origin (Fig. 2).

As a result, populations of Askanian red deer have arisen in the Novovorontsovka district of the Kherson region (Garvrilovsky State Hunting

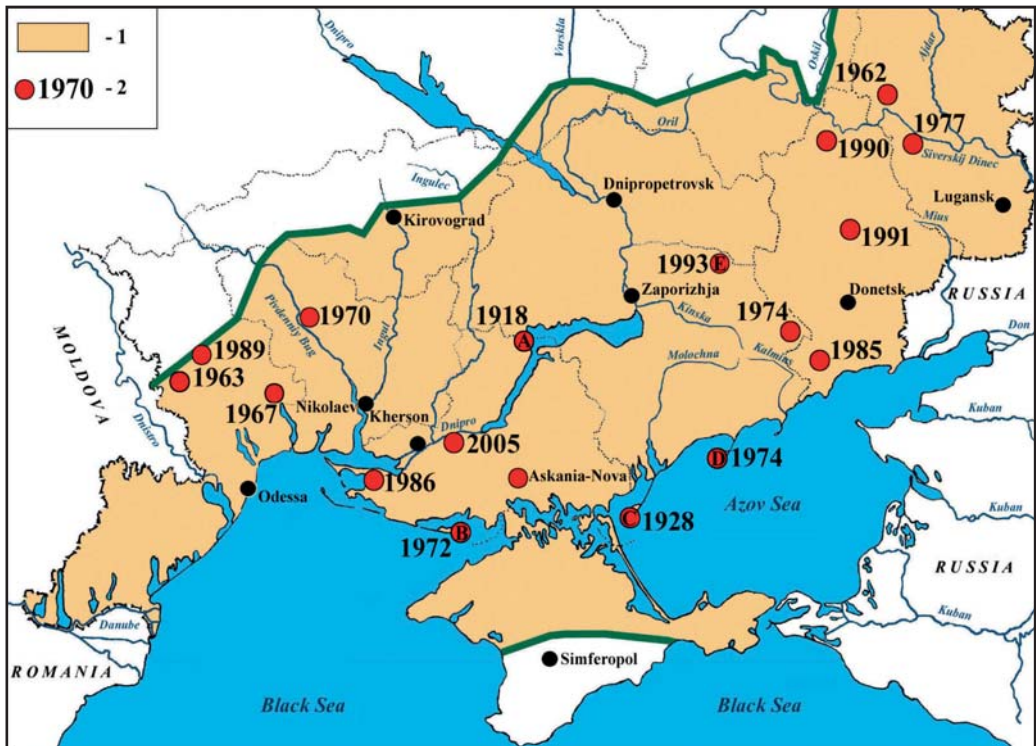


Fig. 2 Locations of red deer introduction into the Ukrainian steppe zone:

1 – Steppe zone; 2 – Location and year of first release of the animal.

A – Novovorontsovka district; B – Dzharlyhach Island; C – Biriuchy Peninsula; D – Obitochnaya Spit; E – Tavria Recreational Park

Reserve), on Dzhyrylhach Island (Dzhyrylhach National Nature Park), on the Biriuchy Peninsula (Azov-Syvash National Nature Park), on Obitochnaya Spit (Priazovsky State Forestry), in some regions of continental Ukraine and the Republic of Moldova, in the Russian Federation and in Kazakhstan. Currently in the Ukrainian steppe zone there are more than two thousand individual Askanian steppe deer. Given that populations of this animal are found in geographical isolation and that the deer has its own significant environmental (VOLOKH, 2003), morphological (KRAVCHENKO, 1971), biochemical (KRAVCHENKO, KRAVCHENKO, 1971) and genetic uniqueness (KUZNETSOVA et al., 2008), it is entirely worthy of the status of subspecies *Cervus elaphus falz-feini*.

Some zoologists (BANNIKOV, LEBEDEVA, 1972; BANNIKOV, 1975), visiting the Biriuchy Peninsula, home to the largest population of such deer, expressed the opinion that by general appearance and antler structure the deer are very similar to the Caspian subspecies. Here they saw animals with simultaneous "European" and "Altai" varieties of antlers which, in their opinion, reduce the trophy hunting value of the Askanian deer. Although at international exhibitions these antlers have repeatedly won gold medals and even awarded the "Grand Prize," in fact this issue has not been specifically studied to date.

Material and methods

Material for this article was provided by results of research we conducted from 1988–2014, in all populations of Askanian red deer. During this long period we were able to measure 510 antlers, of which 234 were paired with a skull (117 pairs) and 276 of were singular. The greatest number of antlers ($n = 391$) belonged to the deer population inhabiting the Biriuchy Peninsula (Fig. 3).

The remainder came from populations on the Obitochnaya Spit, ($n = 65$), Dzhyrylhach Island ($n = 22$), Tavria Recreational Park ($n = 20$), Garvirilovsky State Hunting Reserve ($n = 4$), Askania-Nova reserve ($n = 4$) and Ratsinsky State Hunting Reserve ($n = 4$) located in the Mykolaiv region.

Several forms of antler are found in red deer, differentiated by curvature of the beam, their relative arrangement, and crown structure. Although German hunters identified 6 main types (UECKERMANN, 1960; WAGENKNECHT, 1978), Soviet zoologists V.G. GEPTNER & V.I. TSALKIN (1947) distinguished 11. However, they stipulated that only three are clearly apparent: Central European, Maral-type and Hangul-type. However, when studying Askanian red deer, characterized by a wide variability of antlers, we must note that this classification system failed. To clarify this issue, over 900 photographs have been taken in the central areas of this animal's habitat. Compilation of the data collected through these means allowed us to identify 7 types of Askanian red deer antlers. As this trait is caused exclusively by genotype, this simplified monitoring the population's genetic structure without resorting to complex and expensive methods.

The trophy value of Askanian red deer antlers was evaluated by the Madrid Formula (BRIEDERMANN et al., 1977) and their dimensions were evaluated by the methods of the International Council for Game and Wildlife Conservation (CIC), used in many countries around the



Fig. 3 Measurement of deer antlers on the Biriuchy Peninsula (Azov-Syvash National Nature Park: 04.01.2010) (Photo by V. Demchenko)

world (ZIMPEL et al., 1969; ROSZKOPF, 1974). It involves the measurement of indicators such as length of the beam, brow tine, bay antler and royal antler, as well as the circumference of the pedicle and the beam at the upper and lower parts and the greatest distance between beams. In addition, for the purpose of monitoring trophies, we measured the length of the tines at the antler crowns. In cases when they separated at almost the same point (Fig. 4: A), the length of each was measured from end to base at the level of least recess, located between adjacent tines. If the crown tines were arranged dichotomously and one of them had a type of inclined plane with sizes of different length (Fig. 4: B), we measured the longest. Where at the crown some tines appeared to be primary and others secondary, their measurement was produced as shown in Fig. 4: C). In cases where the terminal part of the antler had a complex spade-like shape (Fig. 4: D), the length of separately spaced tines (right) was measured from the base and the length of the others from the least recess between adjacent tines to their ends. Over many years we have managed to gather

quite an extensive dataset on the development of Askanian red deer antlers. However, since most of them (54,1 %) were found and measured after shedding, it is not possible with a sufficient degree of reliability to sort the data by age groups. Since there is a close positive correlation between the antlers' mass, length, number of tines, circumference at the pedicle and the age of the deer (LOCKOW, 1985), we were able to sort the antlers based on the animal's age based on these characteristics. Among these, circumference at the pedicle was considered primary because it has a relatively small variability among representatives of different ages (SCHREIBER, 1993). This method involves comparing the measurements of single antlers with identical ones near the skull of the deceased or procured animal, whose age was determined by known methods (BRIEDERMANN et al., 1977; SHOSTAK, 1988).

As a result of this approach, antlers with a pedicle circumference within the range of 11,4–21,2 cm, with few exceptions, were classified as animals aged 3–5 years and with a circumference of 21,2 cm and above classified

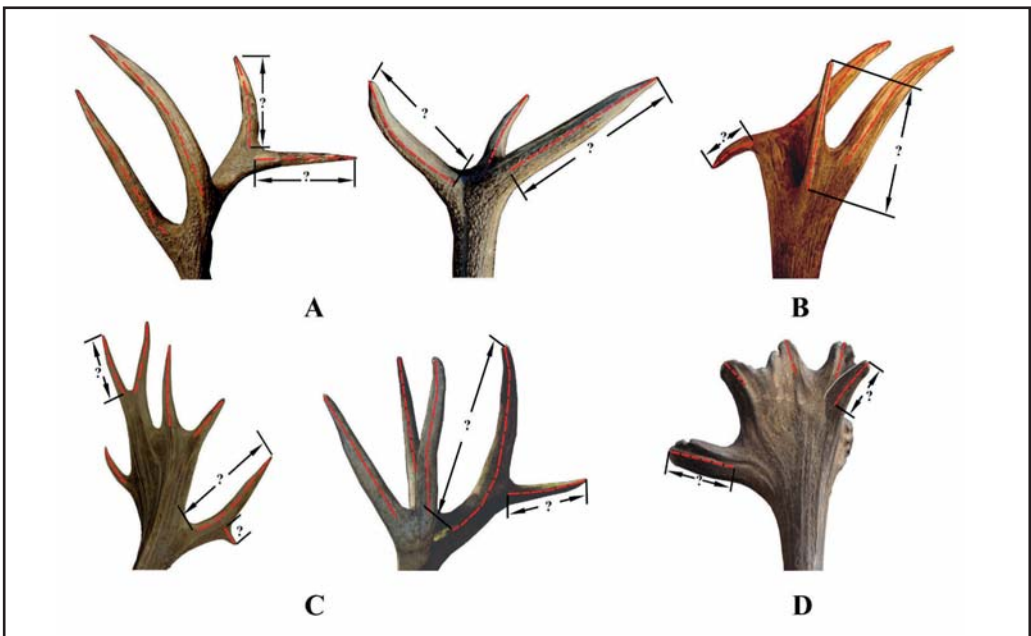


Fig. 4 Length measurement of crown tines: A – Equivalent tines; B – Typical tine and tine with sides of different lengths (center); C – 5 equivalent (left) and 2 unequal tines (right); D – 4 unequal (left) and 1 separate tine (right) in a spade-shaped crown

as older. Of course, to perfectly prevent an erroneous classification this way is impossible. However, it seems that through careful selection of material for calculations, long-term observations of the animals in nature and the inclusion of a fairly large number of animals whose age we were able to ascertain allowed us to reduce the number of likely errors to a minimum.

The results of this research, by necessity, were processed using the computer program package «CSS» from Microsoft-Corporation. In the majority of cases, comparison of animals with different characteristics yielded a confidence level of 95 % ($p = 0,05$).

Antler Types

We have found 7 different types of Askanian red deer antlers: rounded and heart-shaped, rounded and basket-shaped, straight and moderately-spaced, nearly straight and narrow, crooked and wedge-shaped, rounded and widely-spaced, straight and widely-spaced. The majority of

these types are also found in other subspecies of red deer (*elaphus*, *montanus*, *hippelaphus*, *brauneri*), except, perhaps, the last (Fig. 5).

Our research conducted in the Azov-Syvash NNP in the early 21st century showed that in the population of red deer on the Biriuchy Peninsula, despite the variety of types, most often encountered were males with the following types of antlers: (B) rounded and basket-shaped, (E) crooked and wedge-shaped, (F) rounded and widely-spaced (Table 1).

Significantly rarer among deer of Askanian origin are the (A) straight and moderately-spaced and (C) nearly straight and narrow antlers, common in deer of Western and Southern (LINKE, 1957). Most peculiar are the (G) straight and widely-spaced antlers. Although they occur infrequently, they are characteristic of Askanian Maral. Many Askanian deer antler beams (39,3 %) are positioned at an angle of 100–122° relative to one another. Typical for thoroughbred Marals (34,1 %) is an angle of ~90° and for a fairly significant number (26,6 %) the angle is more acute (Fig. 6).

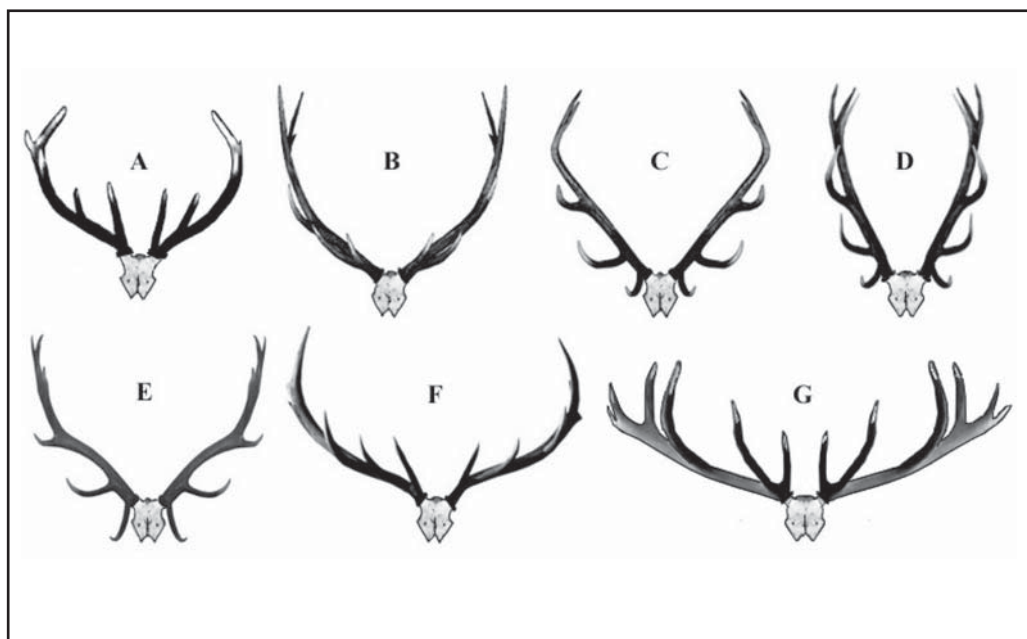


Fig. 5 Types of Askanian red deer antlers: A – rounded and heart-shaped; B – rounded and basket-shaped; C – straight and moderately-spaced; D – nearly straight and narrow; E – crooked and wedge-shaped; F – rounded and widely-spaced; G – straight and widely-spaced

Table 1 Distribution of deer by antler type on the Biriuchy Peninsula from 2008–2014 by %

Year	A (n = 58)	B (n = 235)	C (n = 55)	D (n = 20)	E (n = 321)	F (n = 215)	G (n = 93)	Number of individuals	
								Abs.	%
2008	6,1	32,7	7,1	3,1	25,4	22,5	3,1	98	100,0
2009	9,3	19,5	8,2	2,1	36,3	12,3	12,3	292	100,0
2010	3,9	10,2	4,3	1,2	39,8	28,4	12,2	254	100,0
2011	3,9	9,8	2,0	2,9	41,2	33,3	6,9	102	100,0
2012	3,6	78,3	3,6	1,2	3,6	7,2	2,5	83	100,0
2013	1,3	46,9	2,5	2,5	25,3	17,7	3,8	79	100,0
2014	7,9	9,0	6,7	2,3	27,0	34,8	12,3	89	100,0
<i>Total:</i>	<i>5,8</i>	<i>23,6</i>	<i>5,5</i>	<i>2,0</i>	<i>32,2</i>	<i>21,6</i>	<i>9,3</i>	<i>997</i>	<i>100,0</i>



Fig. 6 Variety of Askaniya Maral antlers by the arrangement of their antlers. (Azov-Syvash NNP, Biriuchy Peninsula: 07/05/2009) (Photo by A. Volokh)

Because the above phenotypes are hereditary in nature, their relative frequency largely reflects the genetic structure of red deer populations. In 1934 a female Wapiti was brought to the Askania-Nova reserve, which after mating with a Maral gave birth to a hybrid male. Among all the deer he was distinguished by his large size and by the spade-shaped crown of his antlers. From 1946–1950 he was the main progenitor in the Askaniya population (TREUS, 1968). This male's influence was expressed in descendants' antlers, which formed four large tines with

a sharp rearward curvature at the top of the beam, typical of elk, as well as flat crown tines. These features can still be found in some deer of Askaniya origin within all Ukrainian populations. It should be noted here that the photo of antlers with four long tines and upper beam curved back is from P. MATSCHI's excellent article (1907), which investigated the antlers of several deer in the vicinity of Lake Teletskoye in Altai. Consequently, which has had the greater influence on Askaniya deer: Siberian Maral or American Elk – is difficult to identify ...

Antler Size and Formation

The formation of first antlers in deer is associated with the activation of hormonal activity and completion of puberty, which in the areas of our research takes place in the last ten-day period of April and in early May. This time correlates with intensive vegetation and a sharp increase in the concentration of natural forage. This is very important for deer of all ages on sea spits and islands, which live on the verge of life and death in extreme years after periods of depression in winter and early spring. But particularly important for young deer is the concurrence of antler formation and the seasonal increase in plant community productivity, since they experience rapid growth at this time and thus require a large amount of metabolic energy.

Given that velvet antlers have the highest growth rate, already around May 1–16 many juvenile males have antlers 5–10 cm or even 10–15 cm long, although some deer at the beginning of the second ten-day period of May have velvet antlers 3–7 cm long. The growth of first antlers in the majority of Askanian steppe deer usually ends in the last ten-day period of July.

By size they are not particularly different from other deer subspecies (Table 2), but by length, weight, and even distance between antlers they are characterized by very high variability. In particular, in the areas of our research the maximum antler length (53,4 cm) was almost 3 times greater than the minimum (19 cm), which in hunting reserves, where special attention is paid to the cultivation of trophy animals, is not usually observed.

One distinctive feature of Askanian deer is that some juvenile males have, instead of the typical forms, antlers with 1–2 tines 3,4–17,5 cm long. Moreover, the tines can be located at the

terminal end of the beam as well as the location of brow tine formation. The weight of first antlers, measured after shedding, had an average range of 65–221 g, although of 18 shed antlers, 44,4 % weighed 112–120 g, 27,8 % weighed 121–132 g, 16,7 % weighed 65–95 g and 11,1 % weighed 210–221 g.

Askanian maral shed their first antlers in late April–early May. For example, on May 6, 2009 we encountered a herd ($n = 3$) of juvenile males on the Biriuchy Peninsula. Two of the deer had the beginnings of antlers 1–2 cm long, and one had not yet shed his antlers, which reached ~22–25 cm in length. Interestingly, on the territory of the Mordovian State Nature Reserve (Russia), which has rather harsh climate conditions, in most cases Askanian maral shed their first antlers from the second ten-day period of April to mid-May (SHTAREV, 1970).

The development of second antlers, which are formed in juvenile Red Deer during their third year, does not differ significantly from adults. From a significant quantity of analyzed antlers in deer aged 3–5 (Table 3), 12 (6,2 %) had lengths of 42,0–49,9 ($46,1 \pm 0,81$) cm, 24 (12,4 %) had lengths of 50,0–59,2 ($56,3 \pm 0,53$) cm, 50 (25,9 %) had lengths of 60,2–69,8 ($65,3 \pm 0,41$) cm, 42 (21,8 %) had lengths of 70,0–79,1 ($74,1 \pm 0,40$) cm, 51 (26,4 %) had lengths of 80,0–89,8 ($84,9 \pm 0,41$) cm and 14 (7,3 %) had lengths of 90,0–97,3 ($93,2 \pm 0,62$) cm.

On the majority of antlers (94,3 %) were well-developed brow tines, of which 12 (6,9 %) had lengths of 4,8–14,8 ($11,8 \pm 1,07$) cm, 35 (21,0 %) had lengths of 15,2–19,8 ($17,6 \pm 0,24$) cm, 97 (55,4 %) had lengths of 20,5–29,9 ($25,2 \pm 0,27$) cm and 31 (16,7 %) had lengths of 30,0–40,0 ($33,6 \pm 0,58$) cm. At the same time, bay tines were observed in only 69,1 % of antlers. Of those, 11,9 %

Table 2 First antler features in Askanian red deer

Feature	n	M \pm m	Min	Max	Std. Dev.
Antler length (cm)	34	34,4 \pm 1,52	19,0	53,4	8,85
Pedicle circumference (cm)	32	10,8 \pm 0,42	7,2	17,6	2,39
Inside spread (cm)	10	38,7 \pm 2,37	29,0	50,0	38,21
Weight of 1 antler (g)	18	123,2 \pm 9,01	65,0	221,0	7,49

Table 3 Antler features of Askanian Red Deer aged 3–5 years

Feature	<i>n</i>	M±m	Min	Max	Std. Dev.
Antler length (cm)	191	72,5±0,92	42,0	97,3	12,68
Brow tine length (cm)	175	24,2±0,49	4,8	41,0	6,54
Bay tine length (cm)	132	20,0±0,77	0,7	36,0	7,98
Royal tine length (cm)	171	22,4±0,45	1,8	38,3	5,92
Pendicle circumference (cm)	191	17,1±0,16	11,4	21,2	2,17
Lower antler circumference (cm)	167	12,3±0,16	7,7	17,5	1,99
Upper antler circumference (cm)	162	10,7±0,16	6,4	16,3	2,03
Number of crown tines	230	2,1±0,07	1	6	0,90
Number of tines on 1 antler	191	4,6±0,08	3	9	1,10
Crown tine length, from 2 cm	226	19,1±0,67	2,3	50,0	10,05
Inside spread (cm)	45	61,8±2,27	33,1	86,8	15,25
Weight of 1 shed antler (kg)	125	1,37±0,07	0,20	3,49	0,80
Weight of antler pair with skull (kg)	26	3,41±0,18	1,62	4,69	0,93

where very short with lengths of 0,7–10,0 (5,7±0,90) cm, 33,0 % had lengths of 10,1–20,0 (15,1±0,40) cm, 45,9 % had lengths of 20,1–30,0 (24,8±0,37) cm and 9,2 % had lengths of 30,1–40,0 (32,2±0,57) cm. On most antlers 3–5 tines were observed and on only a small portion (19,5 %) were there 6–9 tines.

Among singular antlers, 12 (9,6 %) weighed 0,20–0,50 (0,35±0,03) kg, 42 (33,6 %) weighed 0,5–1,00 (0,80±0,02) kg, 31 (23,8 %) weighed 1,01–1,50 (1,27±0,03) kg, 14 (11,2 %) weighed 1,51–2,00 (2,30±0,05) kg, 13 (10,4 %) weighed 2,01–2,50 (2,96±0,05) kg, 9 (7,2 %) weighed 2,51–3,00 (2,96±0,05) kg and 4 (3,2 %) weighed 3,01–3,50 (2,28±0,05) kg. The weights of antlers with skulls were distributed as follows: 5 (19,2 %) weighed 1,60–2,00 (1,90±0,08) kg, 7 (26,9 %) weighed 2,01–3,5 (3,11±0,17) kg, 8 (27,0 %) weighed 3,51–4,00 (3,82±0,06) kg and 7 (26,9 %) weighed 4,01–5,00 (4,40±0,08) kg.

In juvenile ages Red Deer experience antler and tine growth at a rather high speed. The features specified above have an unusually high variability, taking into account the animals' individual characteristics as well as the uneven start time, since the shedding of first antlers and beginning of the second antlers' growth takes place over nearly 1 month. At the same time, the metrics of weight and circumference, which characterize

the growth of horns in thickness, change significantly less.

Among juvenile male Askanian maral aged 3–5 years, most often the antlers terminate in one (29,6 %), two (40,2 %) or three (23,3 %) tines, usually arranged along the sagittal plane (Fig. 7). Very rarely (6,9 %) do the antlers of the examined deer terminate in 4–6 tines. By length they are distributed as follows:

1,7 % with lengths up to 2 cm, 18,3 % with lengths of 2,1–10,0 cm, 39,6 % with lengths of 10,1–20,0 cm, 27,4 % with lengths of 20,1–30,0 cm, 9,3 % with lengths of 30,1–40,0 cm and 3,7 % with lengths of 40,1–50,0 cm.

Interestingly, single terminal tines had the greatest length (32,6±1,59 cm; Min–Max: 14,2–50,5 cm) and dual terminal tines were significantly shorter (17,2±1,77 cm; Min–Max: 0,8–43,3 cm). Even less were the lengths of triple tine crowns (15,1±0,79 cm; Min–Max: 0,6–29,1 cm) and crowns with four tines were very minor (12,6±1,64 cm; Min–Max: 1,2–23,7 cm). Despite the fact that there was no statistically significant dependence ($r = -0,51$; $p < 0,05$) between the number of terminal tines and their lengths, it seems that the genetic mechanism for forming antler crowns allocates a strictly limited quantity of material from which a single large tine or several smaller tines can form.

Antlers in older Askanian steppe deer is distinguished by even faster growth. Naturally, there are determined dynamics in their growth due to differences in age and the year's weather (Fig. 8).

For example:

- March 31, 2010: of 39 males the majority had calcified antlers, 12 of which (30,8 %) measuring 2–3 cm in length.
- April 4: of 8 males, 7 (85,7 %) had calcified antlers and 1 had velvet antlers 1–2 cm long.
- April 26–27: of 21 males, 4 (19,1 %) had calcified antlers and the rest had bump-like velvet antlers 3–7 cm long.
- May 2–3: of 12 males, 2 (16,7 %) had calcified antlers, 2 had small bump-like velvet antlers and 8 had velvet antlers with small tines.
- May 6: of 19 encountered adult males, not one had calcified antlers – all had velvet antlers. However, 2 had the appearance of small bumps (3–5 cm), 2 had slightly forked velvet antlers, 11 had velvet antlers with 3 tines over 20 cm long and 1 had velvet antlers with most tines measuring over 40 cm.

- May 14–16: of 31 males, 3 had velvet antlers 10–15 cm long, the majority had velvet antlers around 30 cm long, 1 had velvet antlers over 40 cm long and 1 had velvet antlers over 60 cm long.
- June 4–8: most males had velvet antlers with 4 tines, with lengths reaching 40–60 cm.

By the end of the last ten-day period of June the majority of males' tine and antler growth was completed, and calcification had slowed. From July 1–10 the majority of red deer are at the peak of their antler development, antler growth stops, and from this time deer begin to shed their velvet. This process has different durations in different populations, depending largely on concentration and quality of forage as well as the animals' physiological qualities. From 1988–2001, during intensive research on the Obitochnaya Spit, almost all adult males' antlers had fully calcified by August 25–27. This was neatly synchronized with the start of the rut, since the first roaring deer could be heard precisely at the end of August. The research conducted at the Azov-Syvash NNP



Fig. 7 Terminal parts of Askanian Red Deer antlers, ages 3–5 years

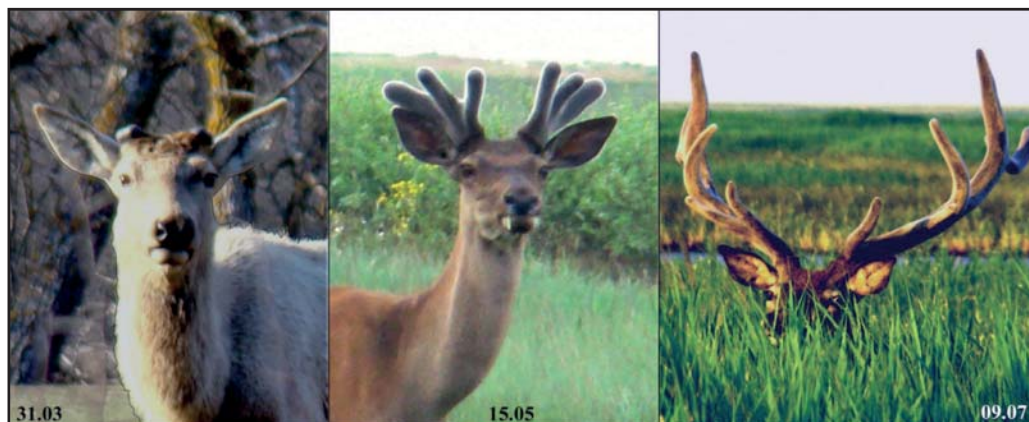


Fig. 8 Dynamics of antler growth and development in adult male Askanian maral (Photo by A. Volokh)

(2008–2014) was marked by the long duration of the velvet-shedding period. For example, the first Askanian maral with partially shed velvet appeared at the beginning of August (Fig. 9), which is typical of other populations. However, despite the height of the rut, there were many deer ($n = 36$) with flaps of velvet hanging from their antlers from September 24–30 and still in the final stage ($n = 17$) from November 17–20. We encountered individual deer with velvet partially shed even later, for example, December 4–11.

This discrepancy is likely a result of a protein shortage for the deer because of the very high density and strong competition for nutrients with other ungulate species. Ultimately, this reduces antler size, deteriorates their trophy value and results in degradation of the animal in general.

Antler shedding in Askanian maral continues for a long time, around $69,1 \pm 5,35$ days. The fastest observed (31 days) was in the spring of 1954, after an unusually long and severe winter during which many males died before the shedding process began. The longest shedding period (94 days) occurred in 1957, after a very warm and almost snowless winter (ISHUNIN, 1960). However, we were not able to reveal a clear dependence between the duration of antler shedding and weather conditions (Table 4).

Unfortunately, a high mortality rate pre-shed was observed in males during harsh winters in

the Soviet era with a relatively low population density and intensive feeding, as well as now in conditions of ultra-high density (40–45 individuals/100 ha). The latter promotes increased consumption of the most high-quality forage plants by numerous fallow deer and red deer, as well as bighorn sheep and kulan (DOMNICH, 2008). In years with severe winters, this leads to a deficiency in the energy exchange, which, given the economic crisis, is difficult to completely eliminate through the acquisition and importation of forage grown in other places. Of course this affects all aspects of life for red deer, not just the duration of antler development. The above is well supported by the fact that Askanian maral living in adverse environmental conditions shed their antlers under different timing. For example, on the territory of the Mordovian State Nature Reserve, deer shed their antlers in March in years with favorable winter climactic conditions. When faced with a shortage of food, this process was delayed by 20–30 days. In years with prolonged cold winters and heavy snowfall, males wintering near haystacks started to shed their antlers on March 1 and the deer living in the pine forest with little forage started to shed theirs March 22–30 (SHTAREV, 1970).

The above durations of antler shedding are also similar for the Askanian red deer inhabiting Dzharylgach Island, Obitochnaya Spit, the Askania-Nova biosphere reserve and other lo-



Fig. 9 Adult deer during final stage of antler formation (Azov-Syvash National Nature Park, Biriuchy Peninsula: 08.03.2009) (Photo by A. Volokh)

Table 4 Duration of antler shedding in deer on the Biriuchy Peninsula*

Year	Shedding Period		Time (Days)	Climate Conditions
	First Antler	Last Antler		
1953	27.02	21.05	83	Winter 1952/53 – warm, little snow
1954	30.03	30.04	31	Winter 1953/54 – very severe, weakened males died before shedding antlers
1955	25.02	20.04	55	Winter 1954/55 – warm, vigorous antler shedding
1956	09.02	06.05	86	February–March 1956 – cold, delayed antler shedding in weak animals
1957	04.03	01.06	94	Winter 1956/57 – warm, little snow
1979	27.02	21.05	83	Winter 1978/79 – warm, little snow
1980	21.02	28.04	67	Winter 1979/80 – warm, little snow
1981	28.02	30.04	62	Winter 1980/81 – warm, little snow
1982	04.03	01.05	58	Winter 1981/82 – cold, early spring
1983	29.02	06.05	67	Winter 1982/83 – warm, little snow
1984	25.02	20.04	74	Winter 1983/84 – warm, little snow

* ISHUNIN, N.I. (1960); RIBIN, E.I. (oral data)

cations in our country. We have studied 56 adult male red deer on the Biriuchy Peninsula, March 27–April 1, 2010, after a long and harsh winter. Of these, a strong majority ($n = 43$) had 2 antlers, 3 individuals had 1 antler and 10 had small velvet antlers 2–4 cm long. This suggests that these deer shed their antlers around March 10–15. Normally, the older animals begin to shed their antlers first, then deer of median age and juveniles last of all.

However, variations do exist. Completely by chance we managed to photograph males of three different ages during this crucial period of the annual biological cycle (Fig. 10). Pictured are a deer (left) aged 7–9 years without calcified antlers but the beginnings of velvet antlers, a deer aged 10–12 years with one left-side antler (center) and a deer (right) aged 5–6 years with both antlers. Interestingly, in Crimea young males shed their antlers from late March–early April and older deer in late February (KORMILICIN, 1970). These dates largely coincide with those of the Askanian red deer.

According to the research results of various zoologists and wildlife managers, among males of certain deer species, antler growth, development, ossification and shedding are regulated by the

concentration of testosterone in the animals' blood. The indicator of activation or inhibition of spermatogenesis is the hormonal activity of the testes. This claim is supported by many researchers who found that the antler shedding in all members of the *Cervidae* family can be induced through castration and premature shedding of antler velvet through testosterone injection. The latter inhibits the velvet's secretion of pituitary growth hormone or creates a spasmodic effect on blood vessels that nourish it, causing the same tissue necrosis. Research on adult red deer antlers in the Askania-Nova biosphere reserve and Biriuchy Peninsula ($n = 112$), first conducted in the 1970s, showed significant similarity to that on the Siberian maral (KRAVCHENKO, 1971). Among their similarities were significantly large inside spreads, long antler length and small numbers of tines (Table 5). In turn, this distinguishes these populations from representatives of other subspecies (MEERWARTH, 1909; GEPTNER, TSALKIN, 1947; LINKE, 1957; DANILKIN, 1999).

In the 1970s antler length in adult Askanian maral often exceeded 100 cm, and the largest recorded was 124 cm, on the Biriuchy Peninsula (ISHUNIN, 1960). All other features were

also of considerable magnitude, which thereby differed through relatively little variability. For antler and tine length it constituted 9,04–20,13 %, and for pedicle and beam length 9,46–17,30 %. The most variable features were the number of tines on 1 antler (20,83 %) and antler weight (30,61 %). Although data on trophy quality was absent from the above-mentioned work (KRAVCHENKO, 1971) in the 1970s it was quite high. This is evidenced by the large values of antler and tine length, weight, beam circumphrences and relatively high number of tines on the beam. In those years great importance was attributed to the containment of ungulate populations within the capacity of the land, carried out by regular shooting of animals of various ages and by capturing fawns. These important activities were actively conducted in subsequent years. Visiting for the first time on the Bir-



Fig. 10 Deer of different ages during antler shed after a harsh winter: 01.04.2010 (Photo by A. Volokh)

uchy Peninsula April 5–6, 1986, we met two herds of elite stags ($n = 19$) and ($n = 37$), almost all of whom could claim medals for themselves. Outstanding trophy males were also registered on the Obitochnaya Spit from 1987–1990. However, since then many years have passed ... The results of our follow-up studies have shown significant deterioration of the trophy quality of Askanian red deer in all areas of its habitat, in most cases resulting from poor management of established resources. On the Biriuchy Peninsula, the most important reason is a very high density of animals, as well as a weakening of selective shooting due to faulty Ukrainian legislation. This strengthens intra- and interspecies trophic competition, which inhibits the growth and development of both the animals themselves and their antlers due to insufficient nutrition. This is confirmed by feeding experiments on farms not only of red deer, but also of European roe deer, fallow deer and moufflon.

Of the significant number of adult deer antlers (Table 6) we studied from 1998–2014, 28 (9,8 %) had a length of 70,0–75,0 ($72,45 \pm 0,32$) cm, 33 (11,6 %) had lengths of 75,1–80,0 ($77,37 \pm 0,29$) cm, 103 (36,1 %) had lengths of 80,1–90,0 ($85,19 \pm 0,31$) cm, 80 (28,1 %) had lengths of 90,1–100,0 ($94,90 \pm 0,31$) cm, and 41 (14,4 %) had lengths of 100,1–117,0 ($105,68 \pm 0,68$) cm. Almost all these antlers (98,6 %) included well-developed brow tines, the length of which in 16 (5,7 %) ranged from 14,5–20,0 ($17,98 \pm 0,36$) cm, in 143 (50,9 %) from 20,1–30,0 ($26,33 \pm 0,23$) cm, in 113 (40,2 %) from 30,1–40,0 ($34,72 \pm 0,25$) cm and

Table 5 Features of adult male Askanian maral antlers, 1970s*

* KRAVCHENKO, R.S. (1971)

Feature	n	M \pm m	Min	Max	Std. Dev.
Antler length (cm)	112	91,53 \pm 0,78	74	109	8,27
Brow tine length (cm)	112	32,51 \pm 0,44	25	43	4,64
Bay tine length (cm)	110	26,49 \pm 0,51	16	42	5,33
Pendicle circumphrence (cm)	111	23,95 \pm 0,21	18	30	2,26
Lower beam circumphrence (cm)	91	20,85 \pm 0,27	12	24	3,61
Upper beam circumphrence (cm)	94	15,87 \pm 0,23	11	20	2,24
Number of tines on 1 beam	82	6,95 \pm 0,16	4	10	1,44
Inside spread (cm)	49	84,14 \pm 1,45	65	105	10,50
Weight (kg)	46	6,64 \pm 0,29	3,5	12	2,03

in 9 (3,2 %) from 40,1–50,0 (43,27±0,93) cm. In the same set, bay tines were observed in only 49.1 % of antlers.

Of those, 6,4 % were very short with lengths of 2,1–10,0 (5,74±1,02) cm, 17,1 % had lengths of 10,1–20,0 (17,08±0,48) cm, 55,7 % had lengths of 20,1–30,0 (25,25±0,32) cm, 20,1 % had lengths of 30,1–40,0 (33,56±0,47) cm and only 1 (0,7 %) reached a length of 43,2 cm. The majority of antlers (61,9 %) had only 3–5 tines, 35,9 % had 6–7 tines, and only a small number (2,2 %) had 8–9 tines. And although in battle it is not so much the number of tines as body weight that gives an animal the advantage, size and placement of especially brow and bay tines are important for protecting the deer's face. In other words, reduction of the lower tines increases a deer's vulnerability during the rut.

Among singular antlers, 17 (11,3 %) weighed 0,43–1,00 (0,87±0,04) kg, 33 (2,0 %) weighed 1,01–1,50 (1,24±0,02) kg, 27 (19,0 %) weighed 1,51–2,00 (1,79±0,03) kg, 23 (15,3 %) weighed 2,01–2,50 (2,31±0,03) kg, 24 (16,0 %) weighed 2,51–3,00 (2,87±0,03) kg, 12 (8,0 %) weighed 3,01–3,50 (3,37±0,04) kg, 8 (5,3 %) weighed 3,51–5,00 (4,11±0,11) kg and 6 (4,0 %) weighed 5,01–8,00 (6,65±0,49) kg. In older males, antler pairs with skulls were distributed by weight as follows: 10 (19,6 %) weighed 3,10–4,00 (3,69±0,31) kg, 17 (33,3 %) weighed 4,10–5,0

(4,44±0,07) kg, 9 (17,7 %) weighed 5,10–6,00 (5,59±0,12) kg, 9 (17,7 %) weighed 6,10–7,00 (6,46±0,13) kg and 6 (11,7 %) weighed 7,10–10,11 (8,85±0,39) kg. For comparison, among Askaniyan maral acclimatized in the Mordovian State Nature Reserve, a pair of Central European-type antlers without the skull typically weighs 6–7 kg, with 6–9 or even 12–16 tines on one antler. A pair of antlers with 6–7 tines and with the skull weighed on average 7–9 kg (SHTAREV, 1970).

Over a long period of time, our research on Askaniyan marals showed a significant decline both in the antlers themselves and in essential elements within all their populations. Moreover, when comparing the obtained results with those from the 1970s, it became clear that for almost all parameters – excluding inside spread, royal tine length, and beam length – these differences remain credible. With a 95 % confidence level we can say that weights of paired horns ($t = 3,2$), brow tine lengths ($t = 4,9$), and number of tines on 1 antler ($t = 6,9$) all significantly diminished. The decline of pedicle circumferences ($t = 12,5$), as well as lower ($t = 22,0$) and upper ($t = 11,4$) beam circumferences, which positively correlate with antler weight, was especially severe. On the other hand, this comparison shows a high increase of inside spreads and beam and tine lengths, indicating a

Table 6 Features of Askaniyan marals aged 6–19 years

Feature	n	M±m	Min	Max	Variance	Std. Dev.
Antler length (cm)	285	88,70±0,61	69,80	116,91	106,79	10,33
Brow tine length (cm)	281	29,77±0,36	14,49	49,88	36,51	6,04
Bay tine length (cm)	140	24,39±0,65	2,10	43,22	58,66	7,66
Royal tine length (cm)	273	26,80±0,38	11,89	44,96	38,55	6,21
Pedicle circumference (cm)	283	20,56±0,17	14,21	29,79	7,98	2,83
Lower beam circumference (cm)	266	14,37±0,12	9,89	21,33	3,76	1,94
Upper beam circumference (cm)	265	12,96±0,13	7,51	20,0	4,17	2,04
Number of crown tines	278	2,83±0,07	1	7	1,19	1,09
Number of tines on one antler	278	5,27±0,06	3	9	1,15	1,07
Crown tine length, from 2 cm*	456	19,05±0,47	2,0	65,0	99,78	9,99
Inner spread (cm)	62	79,46±1,37	44,52	108,51	116,36	10,79
Weight of 1 shed antler (kg)	150	2,26±0,11	0,43	7,99	1,68	1,30
Weight of antler pair with skull (kg)	51	5,37±0,23	3,11	10,11	2,71	1,65

significant dispersion of size. Against this background, there was a decrease in the variability of upper and lower beam circumferences, number of tines and antler weights. All this indicates the stability of these adverse changes.

Usually among deer of Askanian origin the bay tine is located at some distance from the brow tine (Fig. 11), which is characteristic of Siberian maral.

However, a special study revealed that this is not the case in all animals. Of the large quantity of antlers examined, 14,6 % of their tine bases merged together or were arranged at a distance up to 2 cm, which is typical of Central European red deer. For 39,6 % of examined antlers, this value measured 2,3–4,8 ($3,5 \pm 0,18$) cm, 27,1 % measured 6,3–9,8 ($7,9 \pm 0,30$) cm and 18,7 % measured 10,4–15,6 ($12,8 \pm 0,58$) cm. Occasionally among Askanian maral, additional antler growths were developing on the tine bases. Over many years of research, only

14 such instances were observed: 9 on the brow tines, 2 on the bay tines and 3 on the royal tines. The form of antler crowns varies in Askanian deer aged 5–19 years (Fig. 12). Most often it consists of 2 (32,7 %) or 3 (36,9 %) tines, somewhat rarely 4 (15,5 %) or 1 (10,1 %) and very rarely 5–7 (4,8 %). Of these ($n = 463$), 7 (1,5 %) had lengths of up to 2 ($1,0 \pm 0,17$) cm, 75 (16,2 %) had lengths of 2,1–10,0 ($5,9 \pm 0,31$) cm, 198 (42,8 %) had lengths of 10,1–20,0 ($15,8 \pm 0,20$) cm, 143 (30,9 %) had lengths of 20,1–30,0 ($24,9 \pm 0,23$) cm, 19 (4,1 %) had lengths of 30,1–40,0 ($34,2 \pm 0,62$) cm, 14 (3,0 %) had lengths of 40,1–50,0 ($44,2 \pm 0,86$) cm and 7 (1,5 %) had lengths exceeding 50,0 ($56,7 \pm 1,77$) cm. In younger males, singular crown tines were the longest ($45,0 \pm 2,61$ cm; Min–Max: 17,7–58,4 cm), crowns of two tines were significantly shorter ($20,0 \pm 0,75$ cm; Min–Max: 0,8–43,3 cm), crowns of three tines were still shorter ($18,7 \pm 0,66$ cm; Min–Max:



Fig. 11 Arrangement of bay tines on Askanian maral antlers



Fig. 12 Antler crown forms in adult Askanian maral (Photo by A. Volokh)

0,6–65,0 cm) and crowns of four tines were smallest ($14,8 \pm 0,71$ cm; Min–Max: 1,2–36,7 cm).

Antler defects

In connection with the prohibition on usage of game animal resources on Nature Reserve Fund territory (ZAKON UKRAINI, 2009), it became impossible to fully implement selective breeding of Askanian maral in the Asov-Syvash National Nature Park, on Dzharylgach Island and the Obitochnaya Spit landscape reserve, where the main populations are located. This has led to the formation of a certain population of deer with various flaws in antler structure, most often hereditary in nature. Among these defects we have identified 5 groupings (Fig. 13), all of which reduce the trophy value of the deer and can have an adverse effect on their reproduction.

Most often in deer of Askanian origin these defects take the form of asymmetry along the beams and an unequal number of tines on the right and left antlers that visually reinforces the previous flaw.

Antler trophy value

In the 1970s, hunters repeatedly took Askanian maral with horns evaluated at 210–228, 194–208, and 172–186 points, earning gold, silver, and bronze medals, respectively. The biggest antlers, weighing in at 12 kg, were obtained in 1959 on the Biriuchy Peninsula. They were evaluated at 258 points, earning the Grand Prix. At the Second Trophy Exhibition in Moscow (1973), experts evaluated Askanian red deer antlers at 229.06 points, earning a gold medal. They were distinguished by their massive beams and brow, bay, royal, and crown tines – although on the right antler there were only 3 and on the left there were 4. As a side note, in the DDR the trophy-winning buck's antlers weighed 9,85 kg, with a beam length of 104,25 (101,4–107,1) cm, brow tine length of 43,8 (42,1–45,5) cm, royal tine length of 34,05 (29,0–39,1) cm, and pedicle circumference of 29,4 (29,3–29,5) cm. In Hungary the world record-holding antlers reached 14,64 kg, with beams length (left/right) of 126,5/124,8 cm, brow tine lengths of 52,7/55,0 cm, royal tine lengths of 62,7/56,1 cm and pedicle circum-

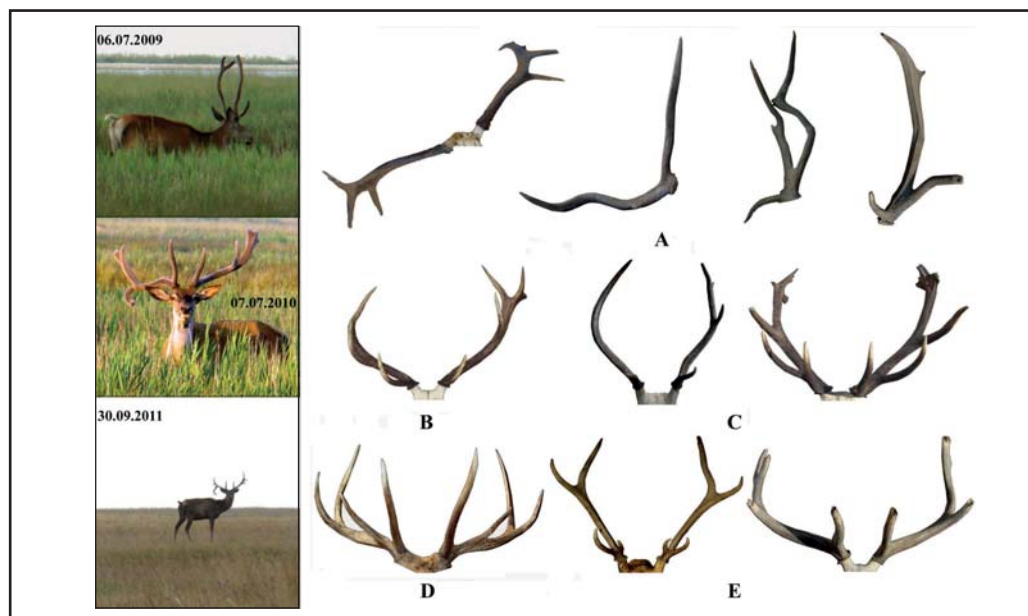


Fig. 13 Typical antler defects in Askanian maral: A – abnormal development of beams; B – asymmetry (of tine number and length); C – misshapen terminal part of tine; D – truncated beams; E – underdevelopment and fragility of tines

ferences of 33,7/33,1 cm. In the first case the antlers were evaluated at 240,79 (gold medal) and the second at 269,89 (Grand Prix) (BRIEDERMANN et al., 1989).

The high quality of Askanian red deer trophy antlers was also observed in the Gavrilovsky State Game Reserve. Here, the animals' habitat in the agricultural landscape, the main forages of which from October to April were winter wheat and barley, did not affect their trophy quality. In 1973, foreign hunters obtained 30 bucks on the reserve territory, out of which 1 pair of antlers was awarded gold, 7 were awarded silver and 11 were awarded bronze medals (ARIDOV, 1973). In other words, among the deer shot, 19 (63,3 %) had a high trophy quality, which is not a bad sign for a game reserve. Of course, the successes above were due to thorough selection, which in later years has weakened.

Of course, the successes above were due to thorough selection, which in later years has weakened. Our results indicate a significant deterioration of trophy quality in all populations of Askanian maral (Table 7). Of 12 pairs of juvenile deer antlers, 16,7 % scored under 100 points and 41,7 % scored 101–110. These animals, removed for breeding purposes, would never have reached trophy conditions. The antlers of the remaining males (41,6 %) were evaluated at 131,96–134,60 points, indicating their potentially high trophy value.

It is significant that of the 22 deer aged 10–13 years, 18 (81,8 %) scored 178,99±1,33 (170,99–188,32) points and could have been awarded bronze medals. In the older group (14–15 years) were many contenders for silver awards (62,5 %), but, given the small quantity of antlers evaluated (n = 5), no serious conclu-

sions can be made. But it is undisputed that, among all the captured specimens, there was not one contender for a gold medal. By comparison, according to chief inspector of the former Azov-Syvash state game reserve E.I. Rybina, of the 28 antler pairs he studied from 1988–1990, 6 (21,4 %) weighed 3,0–5,0 kg, 8 (33,3 %) weighed 5,1–7,0 kg, 9 (37,5 %) weighed 7,1–10,0 kg and 5 weighed 10,1 or more kg. When 18 trophy pairs were measured on the Madrid system, 16 (88,9 %) could claim medals: 7 gold, 5 silver and 1 bronze.

At the turn of the 21st century, even the most outstanding Askanian maral's antlers had only average trophy features. (Table 8).

Despite the deterioration of trophy quality Askanian deer, it should be noted all the same that elite individuals still exist in all Ukrainian populations (Fig. 14), and we must protect them from the adverse effects of various environmental factors as well as encourage their reproduction and the dispersal of their descendants.

On the antlers of such animals the total number of tines reaches 12–16 and forms a crown of 3–6 tines. However, most often these crowns consist of 3–4 flattened tines, broad at the base and the rather long brow, bay, and royal tines are spaced far apart on the beams.

Conclusions

1. Among Askanian maral 7 types of antlers have been classified, of which the most common are crooked and wedge-shaped (32,2 %), rounded and basket-shaped (23,6 %), and rounded and widely-spaced (21,6 %). Most beams (39,3 %) are arranged

Table 7 Age variations in Askanian deer trophies

Age (years)	n	Trophy value (points)*			
		M±m	Min	Max	Std. Dev.
3-4	12	114,32±4,86	86,99	148,50	16,84
5-9	25	159,25±1,09	143,90	166,27	5,44
10-13	22	177,37±1,45	166,81	188,32	6,62
14-15	8	188,79±2,50	188,79	207,44	7,06

* Here and below according to the Madrid system of trophy evaluation

Table 8 Features of prize deer antlers

Feature	n	M±m	Min	Max	Variance	Std. Dev.
Antler length (cm)	56	98,72±1,12	82,13	116,91	70,72	8,41
Brow tine length (cm)	56	34,28±0,79	18,29	49,88	34,71	5,89
Bay tine length (cm)	32	30,69±0,95	20,48	43,22	28,59	5,35
Royal tine length (cm)	56	31,07±0,96	14,51	44,96	51,07	7,15
Pedicle circumference (cm)	56	23,39±0,31	19,69	29,79	5,29	2,30
Lower beam circumference (cm)	56	16,42±0,26	13,04	21,33	3,73	1,93
Upper beam circumference (cm)	56	15,13±0,18	11,53	18,64	1,79	1,34
Number of crown tines	56	3,54±0,15	2	7	1,20	1,10
Number of tines on 1 antler	56	6,05±0,16	4	9	1,51	1,23
Inside spread (cm)	28	87,70±2,41	63,5	122,0	161,91	12,73
Weight of antler pair with skull (kg)	28	6,78±0,30	4,21	10,11	2,43	1,56
Trophy value (points)	28	184,98±1,95	170,99	207,44	106,77	10,33



Fig. 14 Elite Askaniya maral males (Photo by A. Volokh)

at an angle of 100–122° relative to one another, many (34,1 %) at ~90°, and a significant number (26,6 %) at an acute angle.

- Askanian deer's first antlers reached 34,4±1,52 (19,0–53,4) cm in length, their pedicle circumference 10,8±0,42 (7,2–17,6) cm, inside spread 38,7±2,37 (29,0–50,0) cm, and the weight of 1 antler was 123,2±9,01 (65,0–221,0) g.
- Among deer aged 3–5 years, antlers reached 72,5±0,92 (42,0–97,3) cm. On 94,3 % of those, the brow tines measured 24,2±0,49 (4,8–41,0) cm in length. Bay tines 20,0±0,77 (0,7–36,0) cm in length were observed on 69,1 % of antlers, and royal tines 22,4±0,45 (1,8–38,6) cm in length were

observed on 89,5 %. Pedicle circumference ranged from 11,4–21,2 (17,1±0,16) cm. 80,5 % of singular antlers contained 3–5 tines, and the rest contained 6–9.

- Among deer aged 6–19 years, 9,8 % had antlers 70,0–75,0 (72,45±0,32) cm in length, 11,6 % measured 75,1–80,0 (77,37±0,29) cm in length, 36,1 % measured 80,1–90,0 (85,19±0,31) cm in length, 28,1 % measured 90,1–100,0 (94,90±0,31) cm in length, and 14,4 % measured 100,1–117,0 (105,68±0,68) cm in length, 98,6 % of those contained brow tines, the length of which in 5,7 % ranged 14,5–20,0 (17,98±0,36) cm, in 50,9 % ranged 20,1–30,0 (26,33±0,23) cm, in 40,2 %

ranged 30,1–40,0 (34,72±0,25) cm, and in 3,2 % ranged 40,1–50,0 (43,27±0,93) cm. Bay tines were observed on 49,1 % of antlers.

5. Juvenile Askanian maral shed their first antlers in the course of ~1 month, from the end of April through the first third of May, while adults shed their antlers within 31–94 days, from February 27 (the first instance) through June 1 (the last instance).
6. In the 1970s the best antlers were evaluated at 210–228, 194–186, and 172–186 points, corresponding respectively to gold, silver, and bronze medals. Antlers from the Biriuchy Peninsula won the highest awards: 258 points (Grand Prix) and 229,06 (gold medal). This indicates the high trophy value of this animal.
7. From 1988–2014, all antlers examined of deer aged 5–9 years were evaluated at 143,90–166,27 points, outside of medal parameters. Among older deer, some antlers earned silver medals, but there were no contenders for the gold medal.

Summary

From 1918–2010, 415 red deer were resettled on the steppe zone territory of Ukraine, 53.0 % of which were complex hybrids bred in the “Askania-Nova” Reserve. Several populations of deer were created as a result, the largest of which is located on the Biriuchy Peninsula (Azov Sea) and on Dzharlygach Island (Black Sea).

In the course of research from 1988–2014, deer were predominately observed with wedge-shaped (32.2 %), basket-shaped (23.6 %), and rounded and widely-spaced (21.6 %) antlers. In adult deer antler length ranged 70.0–117.0 cm. 98.6 % of them had developed brow tines, and 49.1 % had developed bay tines.

In the 1970s, the best antlers were evaluated at 210–258 points, and from 1988–2014 at 143.90–166.27 points (CIC). This indicates a decline in the trophy quality of deer of Askanian origin, which calls for the implementation of biotechnical measures and selective intervention in all populations.

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Contact:

Prof. Dr. ANATOLIY VOLOKH
Tavria State Agrotechnological University
Department of Ecology and Environmental
Protection
B. Khmelnytski Street 18
72312 Melitopol
Ukraine
E-Mail: volokh50@ukr.net