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Influence of exogenous and endogenous factors on the histomorphology of the red deer interstitial compartment of testicle

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Seasonal changes in histostructure, morphometric and some histochemical parameters of the testis interstitial compartment of 29 adult red deer males - one of the subspecies of red deer, were studied with traditional histological and histochemical methods taking into account the blood content of testosterone and prolactin. The material was taken during the breeding season (October – the second half of the rut period) and during the periods of anestrus: winter (January – February), spring (March – early April) and summer (late June – early July). The mass of the testis and thickness of the tunica albuginea were taken as total indicators. The dimensional fractions of interstitial tissue and seminiferous tubules, their correlation, the dimensional fraction and the quantity of cell elements in general and the quantity of active Leydig cells per conventional unit area separately, the volume of the Leydig cells nuclei were taken as indicators of interstitial compartment functional state. The most pronounced decrease in the mass of the testis is observed in spring and summer, and the thickening of the tunica albuginea in summer. Unlike other animals in red deers there is a significant decrease in the dimensional fraction of the interstitium in the total volume of the testis during one of the anestrus periods (spring). The morphological parameters of the testis endocrine activity of red deer (mass, interstitium specific volume, the quantity and specific volume of active Leydig cells, the volume of their nuclei) reach peak values during the rut period (autumn) with the daylight hours reduction, annual testosterone acrophase and minimum blood content of prolactin. The structural transformations in the testis endocrine compartment have different character during different periods of relative anestrus. In spring, with the increase in the length of daylight hours, the decrease of prolactin and testosterone content, the population of Leydig cells is exposed to the maximum regression, and in summer, with the longest daylight hours, the minimum content of testosterone and the peak value of prolactin, the volume of connective tissue structures of the testis significantly increases.
Keywords: red deer; the testis endocrine compartment; morphometric parameters; histochemical parameters; Leydig cells; seasonal periodicity; hormones

Introduction

Seasonal periodicity, especially pronounced in temperate and northern latitudes, is among the most common phenomena in wildlife. Adaptive rhythmic reactions cover all organ systems of animals. Of great interest are the rhythmic processes in the male gonad, which not only produces gametes, but also functions as an important element of the endocrine system, providing adaptive responses of the body. These processes are distinctly expressed in seasonally breeding animals, the annual reproductive cycle of which consists of the reproduction period (rut) and the period of relative anestrus. These include, in particular, one of the subspecies of red deer - red deer (Cervus elaphus sibiricus Severtzov, 1872), living in the Altai-Sayan mountain region, in southeastern Kazakhstan, and in the Baikal region.
The reproductive cycle of male boreal deer species is characterized by photoperiodic regulation of the short-day type, during which the breeding season falls at the time of shortening of daylight. Their primary photoperiodic effect is mediated through the action of the hormones: melatonin, prolactin, luteinizing and testosterone (Bubenik, 2006). The key role here is played by the hormone of the pineal gland, melatonin, which produces diverse effects in the male's body, including the regulation of

steroidogenesis and spermatogenesis, both directly affecting Leydig cells and indirectly through Sertoli cells and other hormones (Kun Yu et al., 2018).

Hormonal control of the reproductive cycle of male deer is of a cascade nature. The initial link in the cascade chain is melatonin, the peak of which is observed in December, and the minimum - in June. The fall of melatonin concentration in the blood after the winter solstice disinhibits the production of prolactin, the peak of which falls in the middle of June. The next step in the cascade of seasonal regulation of reindeer reproduction is the effect of prolactin on the luteinizing hormone, which stimulates the secretion of testosterone in Leydig cells. A high level of prolactin inhibits LH receptors in Leydig cells, its fall disinhibits them, which leads to enhanced testosterone production (Bubenik, 2006). Thus, these hormones are closely related to the seasonal change in the length of daylight through melatonin. The content of prolactin negatively correlates with the concentration of melatonin, and the content of luteinizing hormone and testosterone is positive. A positive correlation of androgen concentration with melatonin content in seasonally breeding animals of a short day is also indicated by Kun Yu et al. (2018).

The purpose of this study was to determine the structural and functional changes in the endocrine department of the testicle of the deer, depending on the season and the content of hormones involved in the photoperiodic regulation of the reproductive cycle (testosterone and prolactin).

Material and methods

Seasonal aspects of the dynamics of the morphological and histochemical indicators of the endocrine section of the testis were studied using traditional histological and histochemical methods (Microscopic technique ..., 1996) in 29 mature deer males aged 5 to 12 years. The material was taken during the reproduction season (October - the second half of the rut) and at various periods of anestrus: in winter (January - February), in spring (March - early April), and in summer (late June - early July). Each group contained from 4 to 10 animals. The basic morphological parameters of the testis were mass, albumin thickness, interstitial and seminiferous tubular volume fractions, and their ratio (Ukhov, Astrakhantsev, 1983; Avtandilov, 1992). When analyzing we considered the functional state of the interstitium, the volume fraction and the number of cell lines per unit area, volume fraction and number of active Leydig cells (LC) or interstitial endocrinocytes per unit area, volume of LC nuclei (Tashke, 1980, Avtandilov, 1992, Shevlyuk, Stadnikov et al., 1998). The obtained morphometric data were processed by means of standard statistical processing.

Results and discussion

Seasonal mass dynamics of the testicle of the deer had some patterns – it is increased during the reproduction period and reliably (P <0.01) decreased it during anestrus (Table 1).

Table 1. Dynamics of the base morphometric parameters of the red deer testicle during the annual reproductive cycle

Parameter	autumn	winter	spring	summer
Weight, g	127.2±8.7**	91.4±7.2**	57.7±7.0	75.6±14.5
Tunica albuginea thickness, μm	480.3±8.9	497.5±6.5	485.2±9.5 ***	609.4±24.4
Interstitum volume fraction, %	16.5±2.0	19.9±1.5**	11.8±1.7**	21.2±2.8
Seminiferous tubules volume fraction, %	78.0±2.0**	68.1±1.0	71.0±4.5	70.1±2.6
Volume ratio	4.99±0.73	1. 3.58±0.35	5.54±0.57	3.95±0.97

Note: here and for Tables 2-3 differences between the neighboring groups significant at: *P <0.05; **P <0.01; ***P <0.001;

The most pronounced drop in testis mass is observed in the spring-summer period, with the minimum in spring; although the differences between spring and summer are not significant. Similar data on the dynamics of the weight of the testes of red deer are reported by Hochereau-de-Reviers & Lincoln (1978) and Lunitsyn (2004). The thickness of the tunica albuginea, on the contrary, increases in summer to about 600 microns; in the rest of the seasons, it remains approximately at the same level (about 480–500 microns).

For the seasonal dynamics of the ratio of interstitial volumes and seminiferous tubules in the testicle of the deer, the most characteristic is a significant decrease in the interstitium volume fraction (0.001<P<0.05) in one of the periods of anestrus (spring). We associate this feature of the deer with a relatively weakly pronounced seasonal dynamics of the diameter of the seminiferous tubules, on which the volume of tubular tissue in the testis depends (Kudryashova, 2010). In other animals during the regression of the testis, the relative volume of interstitial tissue increases, which coincides with a significant decrease in the diameter of the seminiferous tubules (Cellarius et al., 1986, Shevlyuk et al., 1998).

Thus, the minimum values of the interstitium volume fraction coincide with the seasonal regression of the testis mass. In general, the seasonal variability of the basic parameters of the testis is not pronounced as in other deer (Fig. 1).

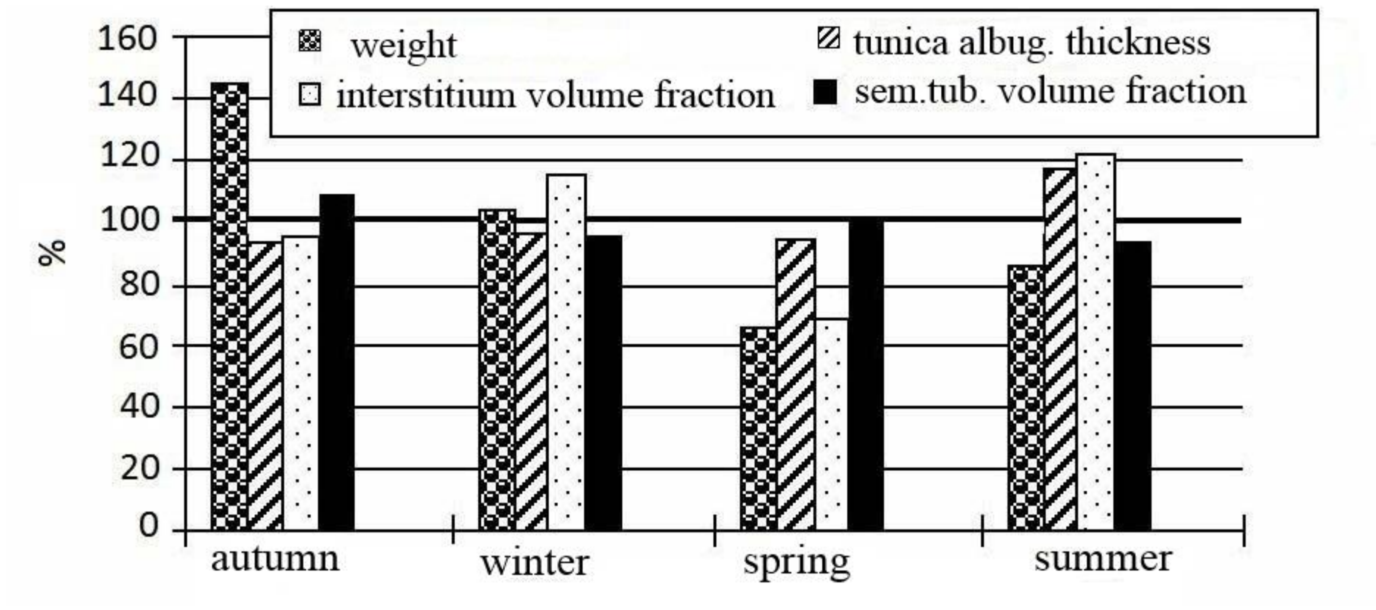

Figure 1. Seasonal dynamics of the base parameters of the red deer testis (% to the average annual value).

When analyzing the parameters of the state of the interstitial division, we noted the seasonal differences in the ratio of cellular and stromal components of the interstitium (Table 2).

Table 2. Morphometric parameters of the interstitial tissue of the testis of adult red deer during the annual reproductive cycle

Parameter	autumn	winter	spring	summer
Cells per area unit	48.1±1.2***	37.2±1.4	37.4±1.3	35.3±1.0
Volume fraction of cells in the interstitium volume	62.1±1.4***	43.6±2.3*	36.4±1.1*	32.5±1.1
Active LC per area unit	15.9±0.7*	12.9±0.7***	2.9±0.3**	5.7±0.5
Volume fraction of LC in the interstitium volume	33.0±1.4***	16.3±1.4***	4.6±0.6***	9.5±0.7

The volume fraction of cellular elements reaches is maximum in the fall, during the rut and begins to decline in the winter. This trend continues until the period of preparation for the rut (summer). Accordingly, the dynamics of the volume fraction of non-cellular components of the stroma has a reverse character: the volume of connective tissue increases significantly during the period of anestrus, especially in the spring-summer season.

Compared to the rut, the number of cellular elements per unit area decreases from the rest of the year (from 48 to 35–37 cells), while remaining almost stable.

Stereometric indicators of the seasonal activity of Leydig cells also show maximum values during the rut period and decrease in other seasons. Thus, the volume fraction of these cells is more than 30% in autumn, and it decreases by 2 times in winter and drops sharply (almost 6 times compared to autumn period) in spring, reaching an annual minimum. In summer, this parameter starts to increase again.

A similar dynamics is characteristic of the number of Leydig cells that are morphologically identified as active. The maximum number of secreting cells per unit area falls on the rut period. In winter, their number somewhat decreases, then there is a sharp drop in their numbers in spring, and by the velvet cutting it gradually begins to recover.

In fall, the active Leydig cells make up about 1/3 of all interstitium cells; their volume fraction is estimated to be significantly higher - more than half of the volume fraction of all cells. In winter, this parameter decreases by 2 times, while their number decreases less significantly. This indicates the predominance of large cells during the rutting period and a decrease in their size in winter, which coincides with the results of karyometric analysis. In summer, the recovery of the activity of Leydig cells begins, which is reflected in a significant ($P < 0.001$) increase of corresponding indicators.

Thus, the number of active interstitial endocrinocytes and their share to stroma volume vary during the year more significantly than similar indicators common to all cellular elements of the interstitium (Fig. 2)

It should be noted that we have not identified mitotic divisions in the endocrinocyte populations of the testicle of mature red deers in all studied seasons, which coincides with the data of Shevlyuk et al., (2010) and indicates the possibility of redifferentiation of Leydig cells from fibroblast-like interstitium elements.

Cariometric analysis of Leydig cells showed a pronounced dynamics in the volume of their nuclei during the annual cycle. We distinguished 3 groups of nuclei: “small” - up to 31.5 μm3, “medium” - 31.5–100 μm3, and “large” - over 100 μm3 from analysis of the data of the volume of interstitial endocrinocyte nuclei. The heteromorphism of the Leydig cell population, including nuclear polymorphism, has been reported for a number of vertebrates and is considered as an indicator of adaptive gonad reactions (Shevlyuk et al., 2017).

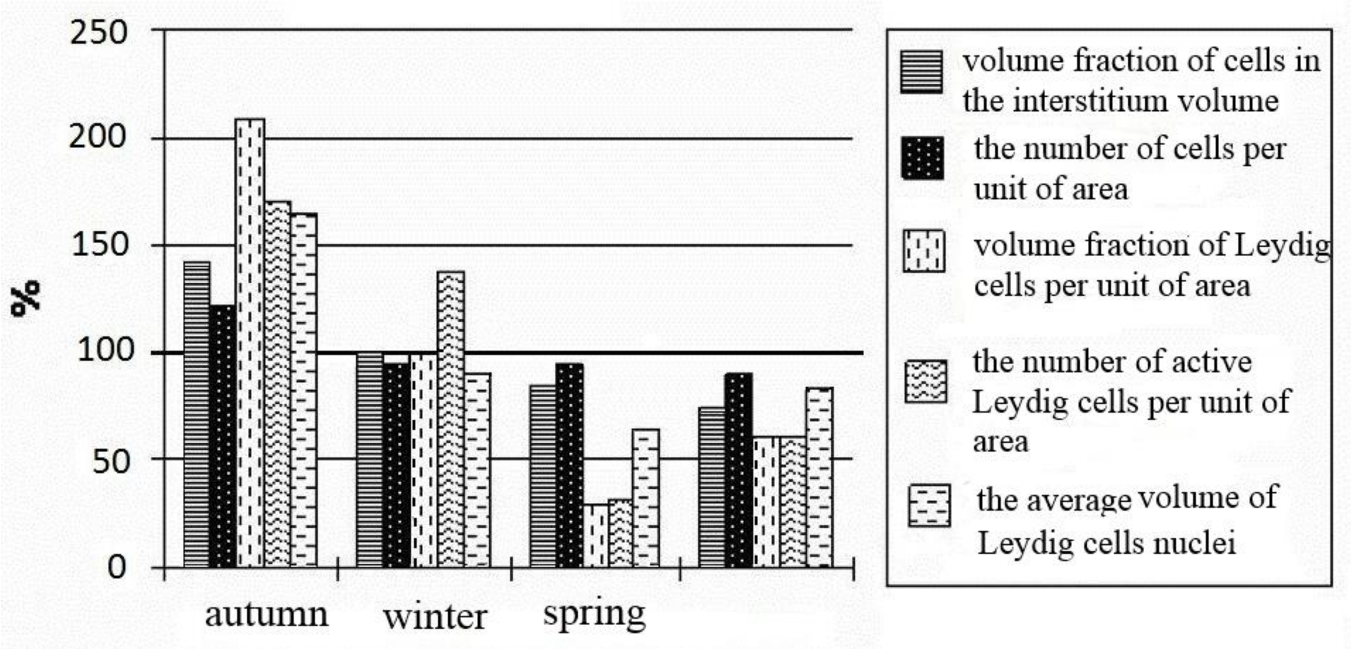

Figure 2. Seasonal dynamics of the morphometric parameters of the red deer testis interstitim (in% of the average annual).

The average nucleus annual volume of Leydig cells is 60.5 ± 0.7 μm3 (lgVc = 1.78). The highest value was registered during the rut - 164.4% of average. In other seasons, the average parameters are significantly reduced. The smallest average size of the nuclei of interstitial endocrinocytes is characteristic for spring and they were 64.3% of the average annual values. In winter and summer, the average nucleus volumes of Leydig cells are larger, but still do not reach the average annual values (Table 3).

Table 3. Cariometric parametres of Leydig cells in testicles of red deer during the annual reproductive cycle, %

Season	Average volume of nuclei (μm)	Ratio of the number of cells with different volumes of nuclei		
		small	medium	large
autumn	99.8±0.8***	3.0±1.5***	46.8±3.8*	50.3±2.3***
winter	49.8±0.9***	36.6±5.3*	63.4±5.3**	4.8±1.4
spring	38.5±1.6***	52.5±4.1*	40.7±3.9**	8.3±4.0
summer	50.1±1.2	29.4±7.2	63.5±5.5	5.9±3.3

Graphic analysis of variation series (Fig. 3) indicates a significant heterogeneity of nuclear populations of interstitial endocrinocytes not only in winter, but also in all the epy periods of the annual cycle.

The variation curve of the logarithms of the volume of the nuclei of Leydig cells during the rut period is clearly isolated and shifted to the right from the annual average value, which indicates an increase in the number of cells with large nuclei. Classical are classes 13 and 14 with a nucleus volume of 92–176 μm (lg = 1.9–2.09). The number of small nuclei of class 3–8 (less than 31.5 μm) is minimal and totals only about 3%. At the same time, the number of cells with medium and large nuclei is very large (46.8% and 50.2%, respectively). Among large nuclei, nuclei of the highest classes (16–18) occupy an important place in excess of 180 μm - they constitute 11%.

During the period of relative anestrus (from December to the beginning of July), shift of the variation curves to the left from the average annual indicator is observed. Nuclear heterogeneity is preserved, but cells with a small and medium volume of nuclei predominate quantitatively.

The winter period is characterized by a decrease in the absolute values of the volume of nuclei. The 9th and 10th classes are modal (35–54 μm3, lg = 1.5–1.69), which together account for 35% of the total number of cells. Leydig cells with nuclei of the upper classes (16-18) disappear, small cells with nuclei of class 2 appear. The total number of small cells (classes 2–8) increases dramatically - up to 27%. This indicates the development of processes of destruction of the glandular tissue of the testis. However, in the group of cells with small nuclei, along with degenerating nuclei, young interstitial endocrinocytes are also found.

The variation curve of the spring period is characterized by greater shift to the left. Class 8 is modal (nuclear volume 28–31.5 μm3, lg = 1.4–1.49), cells with class 1 nuclei appear. The number of cells with small nuclei of the 1–8 class is the largest and makes up almost half of the total number of cells (44.6%). At the same time, cells appear with nuclei of the upper classes, but in very small quantities - about 1%. It should also be noted uneven placement of cells with nuclei of different classes in different parts of the testis. Thus, in spring there is a sharp decrease in the functional activity of the endocrine division of the testicle of the deer.

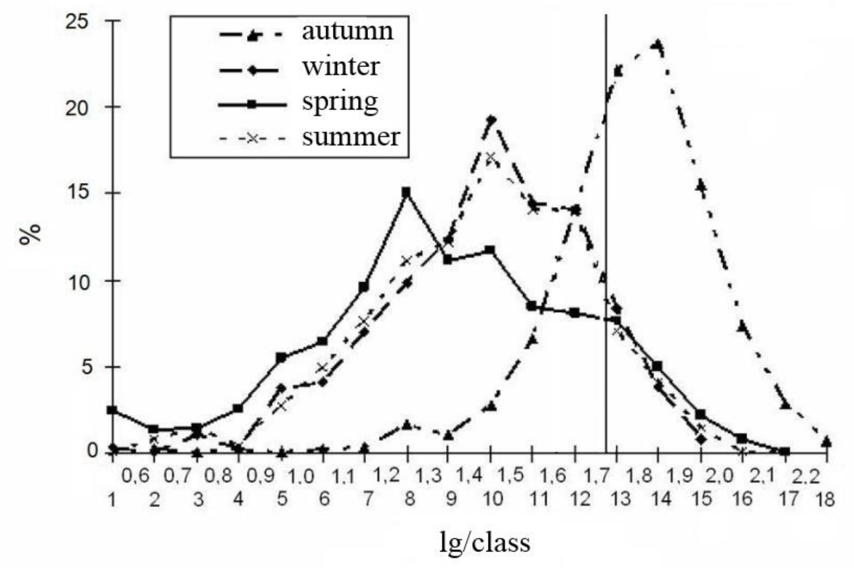

Figure 3. Variational curves of the logarithms of Leydig cell nuclei volume in red deer testicles during the annual reproductive cycle. The vertical line is the annual average.

In the summer, the processes of restoration of the synthetic activity of IE begin, which is expressed in the reverse shift of the variation curve to the right; at the same time, it acquires a great similarity in outlines and position with the curve of the winter period. The mean values of the nuclei volumes are also close, although they are significantly ($P < 0.05$) different. However, the summer nuclear population has its own characteristics: cells with nuclei of classes 1 and 2 disappear, the number of small nuclei of classes 3–8 decreases to 29.5%, large cells of classes 16–18 make up only 0.5%.
Considering the histochemical indices of the interstitial part, we revealed the distinct seasonal periodicity and increased content of sudanophilic phospholipids in the cytoplasm of Leydig cells during and after the rut (Fig. 4). This is one of the signs of active secretion (Lopez-Arranz et al., 1976, Shevlyuk et al., (2010). In spring and summer, their content decreases to the complete disappearance.

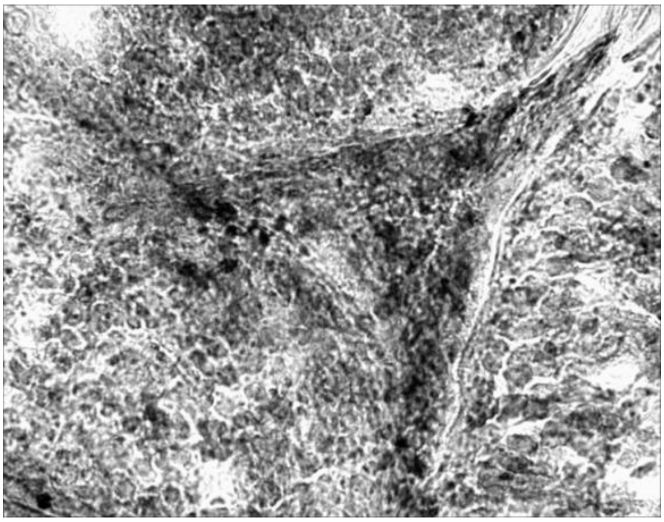

Figure 4. Phospholipids in the cytoplasm of interstitial cells. Red deer is 10 years old. October. Formalin fixation. Coloring Sudan black B. Z. 400

We compared the obtained morphometric characteristics of seasonal cyclical changes in the endocrine section of the testicle to the data from a joint study by Lunitsyn et al. (2003) on the seasonal dynamics of testosterone and prolactin in the peripheral blood of red deer red deers. The maximum values of most morphological indicators of the functional activity of the endocrine compartment are recorded during the rut. First of all, it concerns the mass of the testis. The number of cellular elements is also increased, and their share in the interstitium volume, the largest number of active Leydig cells per unit area is noted, their share in the interstitium volume is 2 times more than in the winter period. The number of cells with large nuclei (more than 50% of the total number) increases sharply, with a corresponding decrease in the number of cells with small nuclei (less than 3%). At this time, the concentration of testosterone in peripheral blood is maximal (6,259 ± 1,583 nmol / l), and prolactin is minimal (25.90 ± 0.52 mMe / l).

In winter, the morphological indicators of the functional state of the interstitium slightly decline. The mass of the testis also begins to decline. The number of Leydig cells with large nuclei decreases sharply, however, the number of cells with medium nuclei is still large, and in general the number of active Leydig cells, compared with autumn, does not decrease very significantly, but significantly (P <0.05). Accordingly, their volume fraction falls 2 times, the number decreases by 1.3 times and the volume fraction of cellular elements in the total volume of the interstitium increases by 1.5 times, which indicates an increase in the proportion of non-cellular connective tissue components. The number of interstitial endocrinocytes with small nuclei increases dramatically, and most of them belong to the involutionary cells. This occurs simultaneously with significant (about 2 times) decrease in the testosterone content in the blood (3.598 ± 0.911 nmol / l) and the annual acrophase of prolactin (84.86 ± 3.85 mMe / l).
In spring, we registered the only significant (in annual cycle, P <0.05) decrease in the specific volume of the interstitium. At the same time, the volume fraction of cellular elements in the total interstitium volume continues (P <0.05), and due to a sharp decrease in the number of active endocrinocytes and their contribution to the stroma volume (P <0.001). In parallel, the volume of the nuclei of interstitial endocrinocytes falls to a minimum and the number of cells with small nuclei reaches the maximum values. These processes occur against the background of a marked decrease in the mass of the testes, which persists in the summer period. The testosterone content practically does not change compared to winter period (3.563 ± 0.352 nmol/l), while the concentration of prolactin sharply decreases (28.91 ± 2.18 mMe / l).
In summer, part of the morphological signs indicate the beginning of the restoration of the activity of interstitial endocrinocytes. The increase in the volume of the nuclei of Leydig cells is carried out due to an increase in the number of cells with medium nuclei; accordingly, the number of active interstitial endocrinocytes per unit area becomes larger. A noticeable increase in the number of cells with large nuclei does not occur. The volume fraction of active Leydig cells in the interstitium volume increases, however, in general, the proportion of cellular elements, as compared with spring, decreases even more (P <0.05). This means that an increase in the volume of the actual connective tissue occurs in the interstitium during the summer period. At the same time, tunica albuginea reaches its maximum. Both of these facts demonstrate a pattern that consists in increasing the volume of connective tissue structures during periods of seasonal involution of the testicle (Raitsina, 1985, Cellarius et al., 1986). Despite the signs of recovery of the endocrine activity of the testis, the testosterone content in the blood drops 19 times compared to the rutting period and reaches an annual minimum (0.340 ± 0.235 nmol/l), while and the amount of prolactin, on the contrary, increases more than twice (65.80±1.10 mMe/l).
When comparing data on the hormone status of red deer with similar data for other deer species, we determined some differences. Thus, in male white-tailed deer, the testosterone content in the blood drops sharply from February and remains at the same level until August (Bubenik, 2006). In males of the red deer, a sharp drop in the concentration of this hormone occurs in summer months, in spring (March) it has the typical winter values (like in January). At this time, the population of the interstitial endocrinocytes of the testis had maximum annual values of depression by the morphological features,. In such circumstances, the source of testosterone can serve as the adrenal cortex, the peak of functional intensity of which in the red deer falls on the spring period (Ovcharenko, Gribanova, 2016).
The summer surge in prolactin content, we registered in male red deers was induced by an increase in the length of daylight and keeps testosterone concentrations at minimal values despite the morphological signs of the resumption of the functional activity of Leydig cells. On the background of the November peak of prolactin, a sharp decrease in testosterone concentration occurs and we registered the processes of seasonal involution in the population of interstitial endocrinocytes and in the interstitium as a whole. In other deer species, the post-rut increase in the concentration of prolactin in the blood was not reported (Bubenik, 2006).

Conclusions

Morphological indices of the endocrine activity of the red deer testis (mass, specific interstitium volume, number of active Leydig cells and the volume of their nuclei) reach peak values on the background of annual acrophase of testosterone and minimal blood prolactin levels during the autumn rut period with reduced daylight. Unlike other animals, the red deer has a significant decrease in the interstitium volume fraction in total volume of the testis during spring anestrus. In different periods of anestrus, we registered different structural changes in endocrine section of red testicles. In spring, when the day length increases, the prolactin and testosterone levels decreased, we observed the maximum regression of Leydig cell population. In summer long light days with minimum testosterone content and a maximum prolactin values, the connective tissue structures of the testicle significantly increase, and the Leydig cell population recovered its functional activity.

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