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Hunting Selectivity and Its Influence on the Structure of Sable Populations in the Cis-Ural Region

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Abstract—The structure of commercial sable samples from the Cis-Ural region was studied taking into account hunting method (shooting or trapping). The proportion of adult animals was found to be significantly lower in samples taken during the first half of the hunting season, compared to the second half, indicating predominant harvesting of young animals. To estimate the degree of hunting selectivity (I), the ratios of demographic groups among shot and trapped animals were calculated. The results confirmed the fact of selective hunting for underyearlings both by shooting (I = 1.49–1.60 for the Cis-Ural region and I = 2.46–3.37 for the Western Sayan Mountains) and by trapping (I = 2.80–4.37), especially during the first half of winter. Samples taken during the second half of the season were characterized by prevalence of adult animals making up the reproductive core of the population (I = 1.43–2.07). It is considered that the process of reproduction in Cis-Ural sable populations in the 1960s to 1980s was stimulated by intensive commercial hunting. To maintain reproduction of sable populations at a safe level, it is necessary to reduce the period of hunting in the first quarter of the year. It is proposed to use the phenomenon of hunting selectivity for managing sable populations, regulating their exploitation, and improving the economic productivity of habitats. Commercial hunting in terms of its impact on the population can act as a factor of conscious or unconscious artificial selection.

Keywords: hunting, selectivity, sable, Cis-Ural region, Sayan Mountains, demographic structure, population, artificial selection

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Hunting is one of the most ancient human activities that initially was vitally important for survival but has largely lost its life-sustaining significance with time. Today, hunting is a profession for relatively small groups of people, with populations of game animals providing the resource necessary to meet their professional needs.

A specific feature of such a resource is that it consists of living populations whose life is governed by biological laws and is part of biocenosis, a more complex living system. Commercial hunting has a dual impact on animal populations: by directly reducing their abundance and, probably, by specifically (selectively) affecting certain intrapopulation groups. If hunting were not selective, the composition of commercial samples would have been always uniform, but actually this is not so.

Animals of different sex and age groups play different roles in the population [1, 2]. Therefore, their selective removal cannot be irrelevant for the population as a system. It is selectivity for animals of different intrapopulation groups that is assumed to account for an indirect impact of commercial hunting on animal populations, including those of the sable.

The sable *Martes zibellina* L. is one of the best-studied species in the game fauna of Russia. It currently plays the leading role in Russian fur trade, with 500–700 thousand pelts being sold every year [3]. There are numerous publications on the problems of sable hunting, but its effect on the populations of this species has relatively recently attracted the attention of specialists. However, it is as early as in the 1940s–1960s that some authors noted that such an effect does take place [4–6], and the same was evidenced by disparity in the results of subsequent studies [7–10].

Animals such as ungulates, fur-bearing carnivores or rodents, fishes, and wildfowl are hunted for sport or commercially, and, sooner or later, the question has been arising as to the deliberate or spontaneous selectivity in their removal from the population and its significance [9, 11–15]. Debates still continue on the consequences of regular selective removal of individuals from animal or fish populations on their demographic structure, genetic and phenotypic characteristics, and reproduction rate.

The purpose of this study was to assess the effect of two basic hunting methods used today on the structure of sable populations (regarding the species as a natural resource).

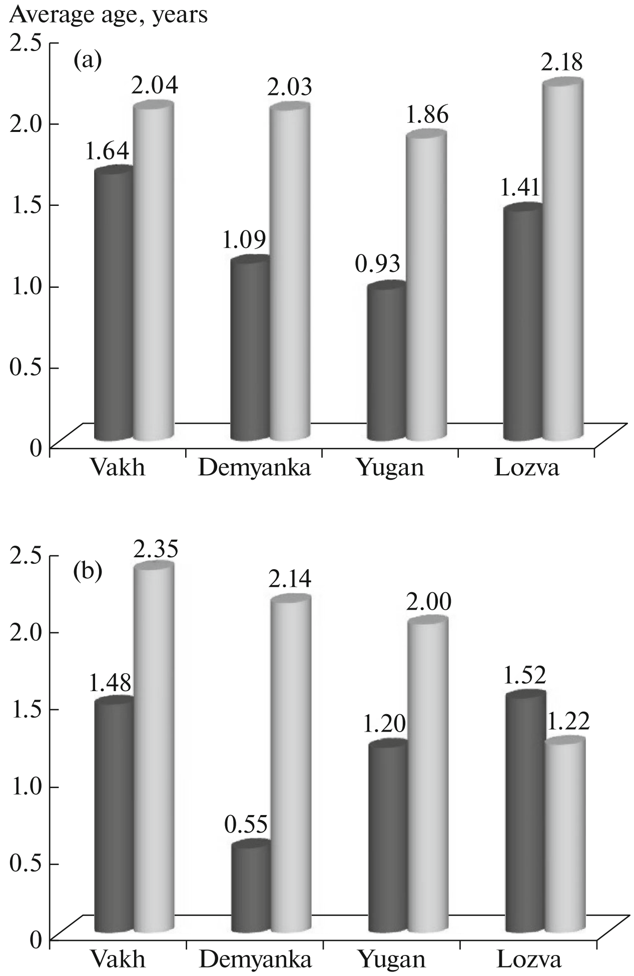

Fig. 1. Average ages of (a) male and (b) female sables in samples from the Cis-Ural region taken during the first half (quarter IV, left bars) and the second half (quarter I, right bars) of the hunting season.

MATERIAL AND METHODS

The material for revealing specific features of hunting methods and their selectivity for sables of different sex and age groups (n = 1769) was collected between 1977 and 1990 in the Cis-Ural region, including Sverdlovsk oblast (Ivdelsky, Garinsky, and Taborinsky districts), Tyumen oblast (Uvatsky district), and Khanty–Mansi Autonomous Area (Surgutsky and Nizhnevartovsky districts). Animal age was determined according to Klevezal [16]. Commercial samples included in analysis were supplemented with data on the method and month of capture for every animal. For comparison, similar material from the Western Sayan Mountains was used (n = 1437) [17, 18].

The age composition of the samples was integrally evaluated based on the index of average age [19, 20], which was calculated by the weighted average formula [17, 21]: $M_a = \sum f_i x_i / n$, where M_a is average age (years), f_i is the number of animals in the ith age group, x_i is age class, and n is the number of animals in the sample. Underyearling were assigned grade 0; yearlings, grade 1; etc. Demographic distributions were compared using selectivity coefficient I [9, 22] characterizing the ratio of demographic groups in the samples.

A simple way to reveal hunting selectivity is to compare catches over a series of consecutive time intervals [9, 23]. However, it should be taken into account that not a single, but two or more hunting methods are used during the season, either alternatively or simultaneously. Therefore, it is methodologically more correct to evaluate the selectivity of each method separately.

In the Cis-Ural region, two methods of sable hunting are used: with dog and gun (or gun alone) and with baited traps, which account for 51.9 and 48.1% of the total catch, respectively [24] (according to our data, 52.6 and 47.4%). Only few hunters set traps on the tracks of sables. Hunting by tracking, with gun and net (without dog), is practiced mainly by the Khanty in the Ob region. All animals in the samples included in analysis were taken either by shooting or by bait trapping, and only these two methods are considered below.

The numerical data were processed statistically by conventional methods in the Statistica 6.0 package.

RESULTS AND DISCUSSION

Analysis of the age structure of commercial samples provided a basis for revealing the age spectra of catches in the first and second halves of the hunting season (quarter IV of the current year and quarter I of the next year, respectively). The data on four study regions (the Lozva, Vakh, Demyanka, and Yugan river basins) over all hunting seasons were pooled into one "Cis-Ural" sample (Table 1). It can be seen that the sample average age differs between quarters IV and I by almost one age class (year); i.e., the catch in the first half of winter consisted mainly of yearlings, and that in the second half, of almost two-year-olds. The proportion of adult animals in quarter I samples reached 48.4% among females and 51.5% among males. Differences in the average age and in the proportion of adult animals between the quarters proved to be highly significant ($p < 0.0001$).

Figure 1 shows data on the average age of animals captured during the first and second halves of the hunting season in the four study Cis-Ural districts which are illustrative of differences in the age composition of corresponding samples. Age differences among males and females were approximately equal (0.74–0.75), but they proved to be greater in Yugan–Demyanka samples (the left-bank Ob region) than in Vakh–Lozva samples (except for females from Lozva).

Selectivity for young animals can be clearly seen when comparing the structure of samples taken during the two periods of the hunting season either in the Cis-Ural region or in the Western Sayan: the proportions

Table 1. Age composition and average animal age (M_a) in commercial samples of sables taken from Cis-Ural populations during the first and second halves of the hunting season

Age group	Males		Females	
	quarter IV	quarter I	quarter IV	quarter I
0	434	160	449	148
1	68	53	67	41
2	37	25	23	21
3	21	9	15	6
4	22	14	16	14
5	15	17	15	16
6	14	28	18	13
7	8	7	7	9
8	10	3	11	9
9	9	7	3	3
10	5	2	4	2
12	7	5	7	5
Total animal numbers	650	330	635	287
$M_a \pm$ SE	1.24 ± 0.10	1.98 ± 0.15	1.09 ± 0.09	1.94 ± 0.17
p_{quart}		<0.0001		<0.0001
Proportion of adults, %	33.2	51.5	29.3	48.4
p_{quart}		<0.0001		<0.0001

Table 2. Proportions of males and underyearling ($M \pm$ SE) among sables taken during different periods of the hunting season

Parameter	Cis-Ural region (n = 2001)	Western Sayan (n = 1537)
Males, %	51.67 ± 1.12	***53.74 ± 1.27***
October–December	50.98 ± 1.35 (1375)	***55.37 ± 1.49*** (1118)
January–February	53.19 ± 1.99 (626)	49.40 ± 2.44 (419)
p_{season}	0.41	0.036
Underyearling, %	***59.52 ± 1.10***	***73.19 ± 0.99***
October–December	***64.51 ± 1.29*** (1375)	***76.65 ± 1.27*** (1118)
January–February	48.56 ± 1.12 (626)	***63.96 ± 1.27*** (419)
p_{season}	0.0001	0.0001

Here and in Table 3, plain and bold italics indicate that differences from the alternative proportion are significant at $p < 0.05$ and $p < 0.01$, respectively; figures in parentheses are the numbers of animals in samples.

of young animals among males and females are significantly higher in the first than in the second half of the season (Table 2). The causes of this phenomenon are well known [25, 26]. Hunting selectivity for male sables was not revealed in the Cis-Ural region as a whole (Tables 2, 3; $p > 0.05$), unlike the situation observed by Klinnikov [27] with sables from Evenkia and in the samples from the Western Sayan in this study (see Tables 2, 3; $p < 0.01$).

Analysis of the results of gun hunting (Table 3) shows that males prevail over females ($p < 0.05$) in samples taken during either the first or in the second half of the season. In the case of bait trapping, the proportion of females in samples from the Cis-Ural region is significantly greater than that of males in quarter IV but becomes approximately equal to it in quarter I. In the Western Sayan, females slightly prevail over males in samples taken at the end of winter, but the difference lacks statistical significance (Tables 2, 3). On the whole, the proportion of males in samples from the Cis-Ural region slightly increases during the hunting season.

Among sables taken by shooting in the Cis-Ural region, the proportion of adult males and females is about 40% during the first half of winter but increases to more than 62% in the second half ($p < 0.001$). Trap-

Table 3. Proportions of male sables ($M \pm$ SE) taken by different methods during different periods of the hunting season

Method	Quarter IV		Quarter I		$p_{IV–I}$	Total
	n	%	n	%		
Cis-Ural region (n = 1769)						
Shooting	771	*53.44 ± 1.80*	301	*54.15 ± 2.87*	0.768	***53.64 ± 1.52***
Trapping	423	*45.86 ± 2.42*	274	51.46 ± 3.00	0.197	48.06 ± 1.89
p_{method}		0.021		0.472		
Total	1194	50.75 ± 1.45	575	*52.87 ± 2.08*	0.431	51.44 ± 1.19
Western Sayan (n = 1437)						
Shooting	510	53.92 ± 2.21	–	–	510	*53.92 ± 2.21*
Trapping	550	***58.00 ± 2.10***	377	48.01 ± 2.57	0.003	***53.94 ± 1.63***
p_{method}		0.190		–		
Total	1060	***56.04 ± 1.52***	377	48.01 ± 2.57	0.003	***53.93 ± 1.31***

Table 4. Proportions of adult male and female sables ($M \pm$ SE) taken by different methods during different periods of the hunting season

Period	Shooting		Bait trapping	
	Cis-Ural region	Western Sayan	Cis-Ural region	Western Sayan
Quarter IV	n = 771	n = 510	n = 423	n = 550
Males	21.40 ± 1.47	12.35 ± 1.44	12.06 ± 1.58	***14.55 ± 1.52***
Females	17.89 ± 1.38	13.33 ± 1.49	10.64 ± 1.52	***7.82 ± 1.16***
Quarter I	n = 301	n = 0	n = 274	n = 377
Males	*31.89 ± 2.69*	–	*24.09 ± 2.58*	20.69 ± 2.09
Females	*30.90 ± 2.66*	–	*16.42 ± 2.21*	15.65 ± 1.89
Entire season	n = 1072	n = 510	n = 697	n = 927
Males	24.34 ± 1.30	12.35 ± 1.44	*16.79 ± 1.42*	***17.04 ± 1.23***
Females	21.55 ± 1.26	13.33 ± 1.49	*12.91 ± 1.27*	***11.00 ± 1.03***
Males + females	***45.89 ± 1.52***	***25.68 ± 1.94***	***29.70 ± 1.74***	***28.04 ± 1.47***

Plain and bold italics indicate that differences between the proportions of males and females are significant at $p < 0.05$ and $p < 0.01$, respectively.

ping affects adult animals to a lesser extent: their proportion increases during the hunting season (quarter IV to quarter I) from 22.7 to 40.5% ($p < 0.0001$) in the Cis-Ural region and 22.4 to 36.3% ($p = 0.0001$) in the Western Sayan (Table 4).

To evaluate hunting selectivity formally, selectivity coefficients were calculated (Fig. 2). They show that the proportion of adults among males and females taken by trapping are approximately equal in both study regions (Table 4). Selectivity coefficients for underyearling in the second half of the season are as follows: $I = 1.14$ for males, $I = 1.96$ for females in the Urals and $I = 1.32$ for males $I = 2.32$ for females in the Western Sayan; the indices for the first half of the season are even higher: 2.80, 4.09 in the Urals and 2.98, 4.37 in the Western Sayan (Fig. 2). In samples taken by shooting, selectivity coefficients for underyearling in the Cis-Ural region are 1.49 for males and 1.60 for females, and in the Western Sayan, 3.36 and 2.46, respectively,

Dul'keit [6] and Nadeev [28] were among the first authors who noted that hunting selectivity may account for mismatch of sample composition to the actual structure of sable population. However, researchers still have not reached a consensus as to the degree and direction of selectivity in sable hunting.

Our data do not confirm the opinion of some researchers that sable hunting is selective for males [6, 27, 29]. Slightly greater numbers of males in catches cannot be regarded as evidence for such selectivity, taking into account that males are generally more active than females, especially at the end of winter. The proportion of males among newborn sables (secondary sex ratio) was estimated at an average of 52.7 ± 0.8% [30]; their proportion in commercial samples taken in 1951–1969 and 1978–1990 in the Transural region ($n = 4110$) was 52.0–52.5% [31]; in the Western Sayan, 50.9–58.7% [32]; and that averaged over species range, 54.5 + 0.08% [25]. Therefore, it may be concluded that certain prevalence of males over females is natural for sable populations [30].

Sable hunting in the Cis-Ural region is selective for young animals [24], as also shown by Kolychev [26] for the Sayan Mountains. Animals aged 7–10 months are the first to be harvested by commercial hunters exploiting sable populations, independently of their intentions and hunting method. It is far more difficult to catch animals comprising the reproductive core of the population [17, 21]. The same is true of old individuals (senex), apparently because of their small numbers and high natural mortality.

The qualitative composition of sables differs between the groups captured by bait trapping and shooting (Tables 3, 4). The proportion of males in trap catches is slightly higher, but the difference lacks statistical significance (see Table 3). With respect to age structure, there is almost no difference between the two groups in the Sayan, but the proportion of young animals among trapped females is higher than among males ($p < 0.01$). In the Cis-Ural region, young males and females in catches by both methods significantly prevail over adults ($p < 0.01$) throughout the hunting season.

Data analysis by periods of the hunting season confirms the trend observed for the season as a whole: young animals are the first to be harvested, regardless of hunting method (see Table 4). Gun hunting in the Cis-Ural region has approximately equal selectivity for young males and females ($I = 1.49$–1.60), but selectivity indices for adult animals in quarter I are different $I_{♂} = 1.43$; $I_{♀} = 2.07$. Selectivity of trapping for underyearling is significantly higher: for males, $I_{qIV} = 2.8$, $I_{qI} = 1.14$; for females, $I_{qIV} = 4.09$, $I_{qI} = 1.96$.

In the Western Sayan, gun hunting is more selective for young males ($I = 3.37$) than for young females ($I = 2.46$), and trapping selectivity is even higher than in the Cis-Ural region: for males, $I_{qIV} = 2.99$, $I_{qI} = 1.32$; for females, $I_{qIV} = 4.37$; $I_{qI} = 2.32$.

Thus, it appears certain that the two hunting methods are selective for young animals, primarily underyearling. In general, the extent of removal by hunting is equal for sables of both sexes, but young females prevail in trap catches.

For effective hunting management, it is necessary to know not only the type of influence of hunting methods in general but also how they affect the population during different periods of the hunting season, giving special attention to probable selectivity for certain age and sex groups [21, 33, 34]. It is also preferable to include in analysis only representative long-term data [35] in order to avoid erroneous estimations creating a risk of overhunting [36, 37].

Fluctuations in the ratio of age and sex groups are higher in trap catches. There is also a distinct tendency toward increase in the proportion of adult animals among males and females taken by both methods during quarter I in the Cis-Ural region ($p < 0.026$) and in the Sayan Mountains ($p < 0.014$) (Table 4). A slight deficit of males in the population will probably have no adverse effect on its reproduction, since even 25% of males is sufficient for successful sable breeding in fur farms.

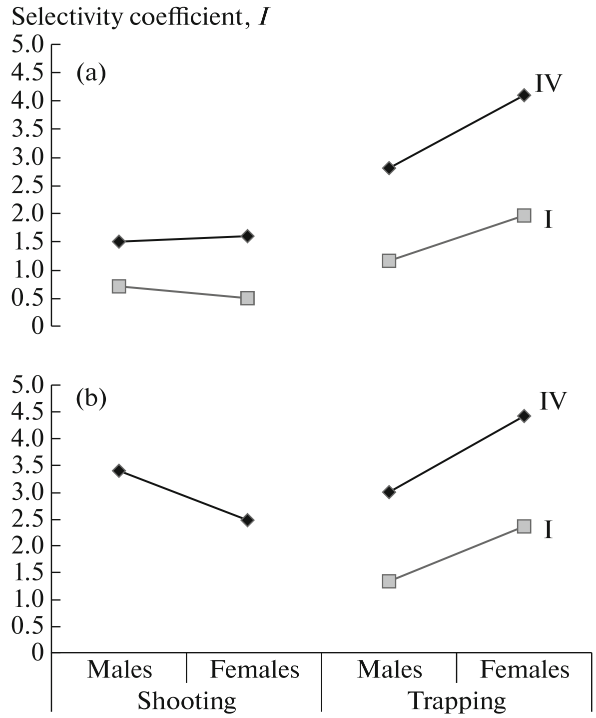

Fig. 2. Selectivity coefficients for young-of-the-year sables from (a) the Cis-Ural region and (b) the Western Sayan taken by shooting and trapping in quarters IV and I.

For fur-bearing animals, hunting is an elimination factor that has an effect not only the abundance of populations but also their spatial structure. Moreover, its effect on animal abundance is determined both directly and indirectly, based on changes in the demographic structure of exploited populations (including sable populations). The indirect effect of hunting is attributed to its selectivity for population groups characterized by physiological heterogeneity [1, 10]. The most significant characteristics of animals depend on their age and sex [34, 38]. Age structure is the most variable parameters of populations [25]. Animals of different age groups differ in life span, mortality, and sexual maturation rate [39–42].

Our calculations of mortality and survival rates in different age groups of sables [17] showed that mortality among animals aged 2–7 years (the reproductive core of the population) averaged 0.286, with their survival (the alternative parameter) averaging 0.714; the survival of underyearling and yearlings averaged 0.340 and 0.596, respectively; the survival of groups 12+ and

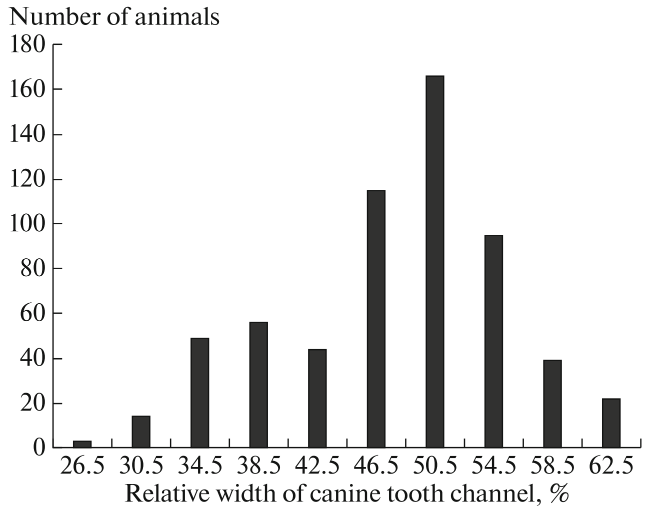

Fig. 3. Distribution of young-of-the-year sables with respect to the relative width of canine tooth canal in samples from the Cis-Ural region taken in 1977–1990.

older was not estimated because of their small size. The proportion of groups comprising the reproductive core in samples are the same or similar to that in the population, which provides the possibility to evaluate the actual structure of the latter. The low survival of two youngest age groups is largely explained by the impact of hunting, while in groups older than 8 years the main role is played by natural mortality [17].

Hunting selectivity leads to disproportional changes in the structure of commercial samples. This is especially true of underyearling: due to selectivity for this group, they prevailed in the sample, regardless of changes in their proportion in the population and of the period of shooting or trapping. Therefore, it should be emphasized that selectiveness of hunting (or hunting method) is a constant parameter, as justly noted by Smirnov and Korytin [9] but denied by Pavlov [35].

Based on analysis of ungulate populations, Rozhkov and Pronyaev [2] equate any type of hunting (even unselective) to artificial selection; i.e., they consider that *any removal from the population can be selective.* This point of view is difficult to adopt, because, based on assumption (or research data) that the removal by a certain method is not selective, an ecologist concludes that its impact on the population is minimal, failing to take into account that we simply do not know what characters are targeted for selective removal; i.e., the ecological essence of this process remains unclear.

Here is an example from our practice. Analyzing the structure of commercial samples of sables from the Cis-Ural region, we revealed a bimodal distribution of male underyearling with respect to the relative width of canine tooth canal, the character by which juveniles and adults can be distinguished from each other (Fig. 3). To find out the cause of this phenomenon, we analyzed the composition of sables within each of the two modal classes, 38.5 and 50.5%. The results showed that the majority of animals in the first class (60.7%) were taken in January to March (on average, in February), and in the second class (84.3%), in October to December (on average, in November). The difference in the width of canine tooth canal averaged 12%, approximately corresponding the degree of pulp cavity occlusion during four months, from October to February. As can be seen in the diagram, the second peak is markedly higher; i.e., the number of underyearling taken in the first half of the hunting season is much greater than in the second half (430 vs. 157 ind., by a factor of 2.74).

Thus, the commercial elimination of underyearling in the first half of the season is significantly higher than in the second half, when they grow 3–4 month older and therefore more experienced. Moreover, catches taken January to February include more animals older than 1 year (2- to 4-year-olds), which comprise the reproductive core of the population. Their prevalence in catches is highly undesirable from the standpoint of rational population management. Rozhkov and Pronyaev [2] explain this effect by different dates of intrapopulation migrations. Indeed, the abundance of commercial resource reaches a peak in autumn (the sable hunting season is from October to February), when active dispersal of juveniles is still underway. Migrations caused by local food shortage also take place in early winter. This is why juveniles are numerically prevalent among sables taken in early winter (when they are mainly hunted with a gun). Similar aspects of commercial elimination are also discussed in publications on other species [43–45].

Our previous analysis of the demographic structure of Cis-Ural sable populations from the 1950–1960s to the 1970–1880s revealed a statistically significant trend toward an increase in potential female fecundity (with the number of yellow bodies increasing from 3.58 ± 0.10 to 4.25 ± 0.08) and in the proportion of underyearling, both over the whole period and at individual stages of the population cycle [31]. This trend appears to be a consequence of commercial elimination. High mortality due to intensive harvesting stimulated reproduction [43, 48], and higher female fecundity gained selective advantage, which provided for population growth necessary to counterbalance high mortality [43, 45]. In our opinion, selective hunting, as well as selection, can cause shifts in the various population parameters (sex ratio, genetic structure, female fecundity, timing of mating and whelping, animal size and weight, etc.) and in the distribution of characters correlated with them. The processes responsible for this are ecological in essence, while hunting acts as a variant of artificial selection [14, 41, 49–51].

As a result of detailed studies on population demographic structure and specific features of commercial elimination of sables, we proposed a scheme of rational exploitation of sable populations based on prompt analysis of the age and sex composition of commercial samples [52], which can be used for hunting management in major hunting enterprises of the Cis-Ural and Ob regions and administrative units of different levels. Other methods proposed for rational population exploitation and development of norms for hunting involve territorial regulation, selection of technologies, dates, and areas for commercial hunting, etc. [30, 53–55]. However, all these approaches are also either based on selective hunting or take it into account. As shown in studies of computational modelling, any method of hunting—provided its intensity does not exceed 53–48% and it is not selective for one of the sexes (especially for females)—will have no destructive effect on the population but is even beneficial, since it provides for a 1.4-fold increase in total production, compared to an unselective method [22, 35, 56].

Thus, commercial sable hunting by two basic methods used in the Cis-Ural region in the first place results in the removal of young animals from the population, while catches taken during the second half of the hunting season contain 40–60% of adult animals. Therefore, it is recommended to shift the onset and ending times of the hunting season to earlier dates in the first quarter of the year. Using different methods in combination with variable dates of hunting makes it possible to regulate the removal of individual belonging to different functional groups within the population. Therefore, commercial hunting can act as a variant of conscious or unconscious artificial selection and cause directed changes in population structure.

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