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Age distribution in sable *Martes zibellina* populations

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Abstract

The results of precise aging of sables from 14 regional populations made for last 30 years are discussed. The age composition was shown to be the most variable characteristics of the sable populations. The juveniles and senex have the greatest rates of mortality. The juveniles (sub-yearlings), yearlings (> 1 year), middle-aged and mature sables, forming the reproductive core (2 – 7 years), and senex (older than 8 years) represent the four separate functional macrogroups of sable populations. Composition of representative samples reflects the true population structure but for reproductive core only. The juvenile sables play the role of »superfluity« in the population; besides, they are hunted selectively.

Zusammenfassung

Altersverteilung in Zobelpopulationen (*Martes zibellina*) – Es wurden die Ergebnisse der exakten Altersbestimmung aus 14 Untersuchungsgebieten – mit Hilfe von einer in den letzten 30 Jahren angewandten Methode untersucht. Es wurde gezeigt, dass die Altersverteilung einer der am meisten veränderlichen Parameter der Zobelpopulationen ist. Den größten Sterblichkeitskoeffizient haben die juvenilen und mehrjährigen Tiere. Juvenile Tiere, einjährige (ein Jahr +), die den Reproduktionskern bildenden subadulten und adulten Tiere (2 – 7 Jahre alt), und mehrjährige (über 8 Jahre alt) bilden in den Zobelpopulationen vier verschiedene funktionelle Gruppen. Die Zusammensetzung der repräsentativen Stichproben widerspiegelt eine echte Populationsstruktur, aber nur für die Tiere des Reproduktionskerns. Die juvenilen Zobel spielen in der Population eine »Ballastrolle« und werden außerdem wahlweise gefangen.

Keywords: age determination, population dynamics, life span, mortality

1. Introduction

Age composition is one of the most variable characteristics of any population (ODUM 1986). It is currently considered to be one of the ways in which populations adapt themselves to changing environment (SCHWARZ 1969). At the same time, the age structure is one of the least studied population characteristics, especially for game or fur-bearing animals, because methods for relatively precise age determinations have not been worked out until recently (e.g. SMIRNOV 1960, KLEVEZAL & KLEINENBERG 1967). Nevertheless, studies on the age structure have been done on a number of game mammals, including sables (e.g. TIMOFFEEV & NADEEV 1955, BAYEVSKY 1956, ZALEKER 1956, 1962, VERSCHININ 1963).

By previous investigations (e.g. SOKOLOV 1979, MONAKHOV & BAKEEV 1981, MONAKHOV 1983), the age structure of sable populations was found to change in time and to differ between the parts of the area, the most changeable parameter being the share of cohorts of under one-year-old animals, i.e. juveniles. However, the old methods of age determination were inadequate for revealing not only the exact age structure of the groups selected, but also such important characteristics as the life span of the sable in the wild.

Unfortunately, the analysis of population age structures by such methods as counting structures in teeth and bones (KLEVEZAL & KLEINENBERG 1967) was not popular amongst researchers interested in sable ecology during that period (KRYUCHKOV 1974, SOKOLOV 1979, BELOV 1980, MONAKHOV 1983, DEVYATKIN 1992). The reason for that might be the complexity of this method.

It may seem doubtful if the determination of population structure based on animals taken in hunting is correct. Now the only accessible and objective method to solve this problem is to test, biologically, the population structure. One cannot say that the structure obtained in an investigation is the same as the true population structure, but there is no doubt that the structure revealed by hunting samples does reflect the true population structure, especially in its dynamics. This method has been used widely by ecologists for many years. MACFADYEN (1965) noted that in a population of wild animals only a selected group could be studied »though data obtained by that method could be very precise«.

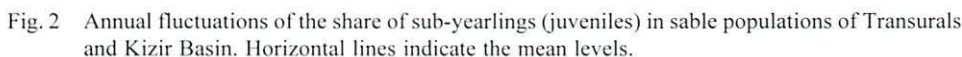
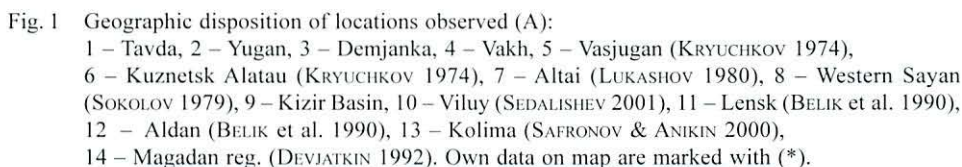
2. Materials and methods

In the present study, the author used his own data to reveal the age structure of sable populations (studied with game-management needs) in the northern Sub-Urals ($n = 2150$) during the period of 1978 – 1990, and in the basin of the River Kizir (the western Sayan, $n = 1765$) during the period of 1977 – 1982. For the analysis, data on age structure obtained by applying the method of KLEVEZAL & KLEINENBERG (1967), which is based on counts of cement layers in the sable canine teeth, were used.

The author has been applying the Klevezal method since 1978 using a basic part of upper (or mandibular) canine tooth. Microscope preparations included 10 – 16 dyed longitudinal sections. The cross-section does not allow observations of annual layers along their whole length. The main difficulty was to determine the age of animals > 1 year and < 2 years old. In some cases, the first annual layer in the canine cement is partially indistinct, or not visible along the whole length (GRAKOV 1981, MONAKHOV 1984, 2004, KLEVEZAL 1988). Such animals could therefore sometimes be determined as juveniles.

»Readability« of annual layers in canine cement can vary depending on the quality of preliminary procedures and dyeing technique, as well as on the equipment used (e.g. microscope, lighting). Sufficient experience, training, and senior colleagues' participation are necessary for successful determination of sable age. It is also desirable to have reference preparations of animals of known age.

In addition, the literature data were used for comparisons (total sample is 11 563 individuals, Tab. 3). All observed regions are shown in Fig. 1. By analysis of age structure, the index of the mean age (M_a) was calculated as a weighted average, according to the formula: $M_a = \sum f_i x_i / n$, where f_i was the number of animals in the x_i age class (0, 1, 2, etc.), and n was the number of animals in the sample(s).



Tab. 1 Age structure and survival rates (SR) in sables of variable age groups from northern Urals and Priobye (in per mille)

Age class	1978–1979	1979–1980	1980–1981	1981–1982	1982–1983	1983–1984	1984–1985	1985–1986	1986–1987	1987–1988	1988–1989	1989–1990	Sum (n=2150)	n'	SR	n" (SR=0.773)
0	386	358	756	581	748	360	310	487	672	756	586	524	627	635	0.199	240
1	250	60	54	231	156	160	123	111	74	104	184	213	125	126	0.440	187
2	92	97	48	33	18	40	121	100	66	26	69	71	55	56	0.777	138
3	92	75	16	10	16	80	138	67	9	15	18	24	27	43	0.759	108
4	90	102	25	23	0	0	52	61	33	15	17	0	33	33	0.776	82
5	45	82	22	26	31	80	69	56	41	15	6	24	32	25	0.776	63
6	45	90	22	56	16	160	34	28	31	25	40	24	37	20	0.794	49
7	0	22	16	10	0	80	17	19	25	8	23	24	15	16	0.759	38
8	0	45	16	7	15	40	52	28	29	8	11	0	17	12	0.776	29
9	0	22	13	3	0	0	34	33	4	8	11	0	11	9	0.776	23
10	0	22	3	13	0	0	17	6	0	4	6	24	7	7	–	18
11	0	10	6	7	0	0	17	0	4	8	6	0	6	6	–	14
12	0	8	0	0	0	0	0	4	4	6	0	48	4	4	–	11
13	0	7	3	0	0	0	16	0	8	2	23	24	7	8	–	1
M_a	1.57	3.05	1.04	1.24	0.61	2.72	2.97	1.96	1.41	0.88	1.49	1.99	1.43			
$\pm SE$	0.27	0.27	0.13	0.13	0.19	0.56	0.43	0.20	0.17	0.10	0.16	0.22	0.05			
Q_{2-7}	364	468	149	158	81	440	431	331	205	104	173	167	199			
$\pm SE$	73	43	20	21	34	99	65	35	26	13	29	57	9			

3. Results

As a result of age determination, we have received annual age distributions from sable populations of the Transurals (Tab. 1) and the river Kizir basin (western Sayan Mts, Tab. 2).

As a rule, the juveniles (born in the current year) dominated in populations (Fig. 2). Their average share was $627 \pm 10.4\%$ and $756 \pm 10.2\%$ in the Transurals and in the basin of Kizir, respectively, and differences between regions were statistically significant ($t_d = 8.86$, $p < 0.001$). However, the share of juveniles was not constant and varied to a great extent, as shown in Fig. 2.

Probably fluctuations of the number of juveniles cause the cycling size of a population as a whole (NAUMOV 1963, MONAKHOV 1968, 1974). Average shares of other age groups in the investigated regions were less variable.

In this study, different aspects of population demography of sables will be considered in comparison with the data by other researchers found in scientific publications.

Tab. 2 Age distribution of the sable population in Kizir basin (1977 – 1982, in per mille)

Age class	1977–1978	1978–1979	1979–1980	1980–1981	1981–1982	Average
0	801	702	682	834	768	756
1	61	106	41	7	35	57
2	36	64	88	19	39	49
3	20	41	34	26	22	29
4	18	29	30	32	26	27
5	23	14	30	29	44	25
6	20	14	41	10	18	20
7	9	8	17	2	4	8
8	7	4	30	16	22	14
9	3	12	0	10	9	7
10	0	2	7	13	4	5
11	2	4	0	0	0	2
12	0	0	0	2	9	2
$M_a \pm SE$	0.67 ± 0.08	0.90 ± 0.09	1.26 ± 0.13	0.85 ± 0.07	1.04 ± 0.12	0.91 ± 0.04
Quota of 2–7 $\pm SE$	126 ± 16	170 ± 17	240 ± 25	118 ± 18	153 ± 24	158 ± 9

4. Discussion

Some factors that determine the age structure of populations, such as life span, mortality, and reproductive properties, need to be discussed.

Life span

The potential life span of a sable is about 20 years, as shown by data from zoos and fur farms (MANTEIFEL 1934, AFANASYEV & PERELDIK 1966, MONAKHOV 1974). Recent studies (SOKOLOV 1979, BELOV 1980) have shown that the age of the oldest animals in the wild is 13 – 20 years, but their proportion in populations is extremely low, i.e. 0.1 – 0.3 %. Amongst the presently studied samples, we found sables of maximally 12 (from the Kizir basin) and 18 years old (from the northern Sub-Urals, own data). There are no animals over 15 years old in nature, or their number is very low.

Cementum layer counts showed that the life span of sables in nature is much shorter than in animals from fur farms. Thus, the existence of animals of 13 – 14 years old in nature can be considered as an extraordinary event. It is generally agreed (SCHWARZ 1959) that the potential life span is hardly ever attained in nature. In fact, only one per mille of sables reaches an age approaching the possible maximum. In reality, the average life period of sables in nature was estimated to be 2.5 – 3.5 years.

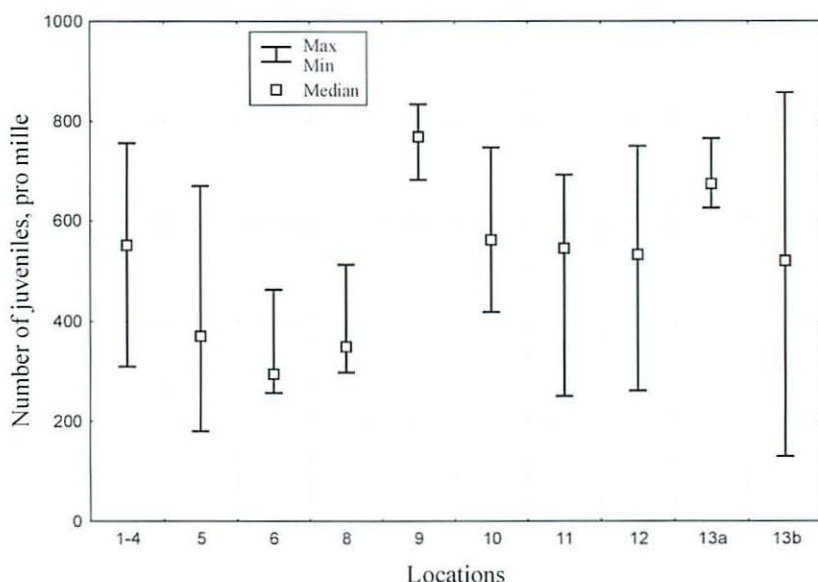


Fig. 3 Dynamics of the share of juveniles in sable populations of Siberia (enumeration of locations as in Fig. 1). Note: 13a – after BELIK et al. 1990, 13b – after SEDALISHEV 2001.

Age structure, mortality and survival

Investigation on samples (Fig. 3, Tab. 3) showed that the proportion of juveniles is very often enormous. This is in contradiction with the natural rate of population growth and litter size observed (see below). This phenomenon could be explained by predominant

withdrawal of juveniles in the hunting process (i.e. selective catching, shooting and trapping) as reported earlier (MONAKHOV & BAKEEV 1981, MONAKHOV 1983) for sable and (SMIRNOV 1983) for other harvested species.

Both data by other researches (MONAKHOV & BAKEEV 1981) and our data (MONAKHOV 1983, 1999, 2004) prove that the age structure is the most changeable characteristic of the population, and this is more pronounced for the younger age groups, especially the juveniles. This fact was also proved by precise determinations of the age and by subdividing the samples into age groups (Tab. 3). Thus, in the total samples, the share of juveniles ranged from 15.2 % in Kizir (Tab. 2) to 44.6 % in the Sub-Urals (Tab. 1), the share of year-old animals 9.9 – 19.6 %, group of 2 – 5 year-old animals 8.5 – 31.5, of 6 year-olds 3.1 – 14.4, and of 7 years and over 3.3 – 15.3 %. In general, groups of young animals, especially juveniles (Fig. 2), determined population fluctuations and age structure cycling all over the species area (Tables 1, 2, 3).

Tab. 3 Age distribution of some sable populations in Russia (in per mille). Enumeration of locations as in Fig. 1.

Age class	Locations (<i>n</i>)										
	1. (321)	2. (634)	3. (430)	4. (765)	5. (859)	6. (537)	7. (914)	8. (3508)	9. (1765)	13. (1477)	14. (353)
0	667	555	664	635	353	305	340	360	756	559	377
1	65	164	133	95	167	181	173	223	57	219	244
2	40	69	50	53	165	169	127	125	49	115	119
3	40	32	14	30	123	143	118	94	29	56	90
4	34	39	22	42	76	86	94	68	27	23	59
5	34	39	24	33	50	50	66	48	25	17	34
6	44	38	31	40	30	47	49	31	20	8	20
7	12	16	17	14	19	13	13	22	8	3	17
8	25	16	16	14	12	4	13	13	14		11
9	3	17	7	14	4	0	4	6	7		28
≥ 10	34	14	22	30	1	2	2	10	8		

Before analysing the age structure, it should be noted that the average age (M_a) characterises not only the age structure of the population, but gives an impression on dynamics in the population size. Thus, the increase in the average ages (Tabs 1 and 2) in 1979/80, 1983 – 1985 and 1989/90 reflect the decrease in the population size and the extending the age spectrum in those years. On the contrary, the lowest values of M_a reflect population rejuvenation and, consequently, the increase of the population size (see Fig. 4). All the above-mentioned is an additional proof of very close connections between dynamics in number, population age structure, and life conditions (SCHWARZ 1960, NAUMOV 1963, MACFADYEN 1965).

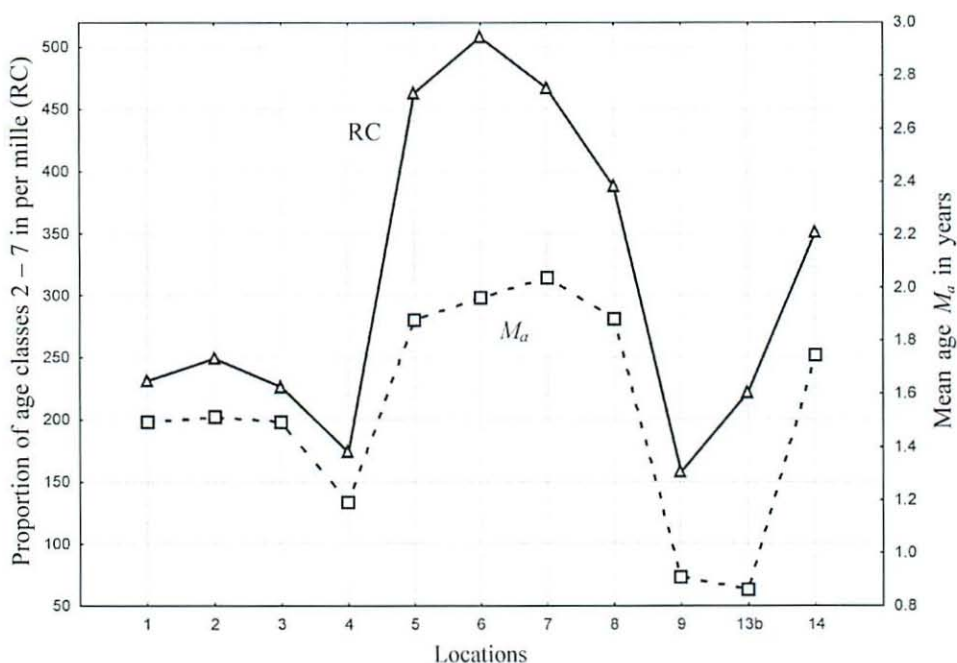


Fig. 4 Variations of the mean age M_a and the share of 2 – 7 years old sables in some Siberian populations (enumeration of locations as in Fig. 1). Note: 13b – follow SEDALISHEV 2001.

Dynamics of the age structure of sable populations in the western Sayan in 1966 – 1970 (SOKOLOV 1979) and in 1977 – 1982 (own data) is combined in Fig. 5. The logarithmic scale is used to give a possibility of correct evaluation of the evenness of decrease from one (younger) age group to another (older) one. In other words, we can evaluate animal mortality and survival from various age groups («current age distribution», see CAUGHLY 1979) and evenness in reductions in their number by hunting. In fact, as CAUGHLY (1979) noted, on the logarithmic scale, the number of animals in age groups decreases linearly by time. Consequently, deviations from the straight line («D» in Fig. 5) in the diagram should mean growing or reducing mortality of animals of a definite age group and selective hunting (in the case of overstepping). In Fig. 5, the line of the age distribution is not straight although it tends to be. Nevertheless, the straight line is an ideal case. The numbers of animals in the age groups from 2 to 8 smoothly decreases, whilst in age groups 9 and older, reductions in number is more abrupt. The above-mentioned facts allow us to conclude that until some definite moment (age), in populations of long-lived species of game animals, mortality is caused mainly by the influence of hunting, and then natural reduction becomes more important. CAUGHLY (1979) found that the curve of age-dependant mortality is of «U»-shape, and this is also proved by data on sables (Fig. 5).

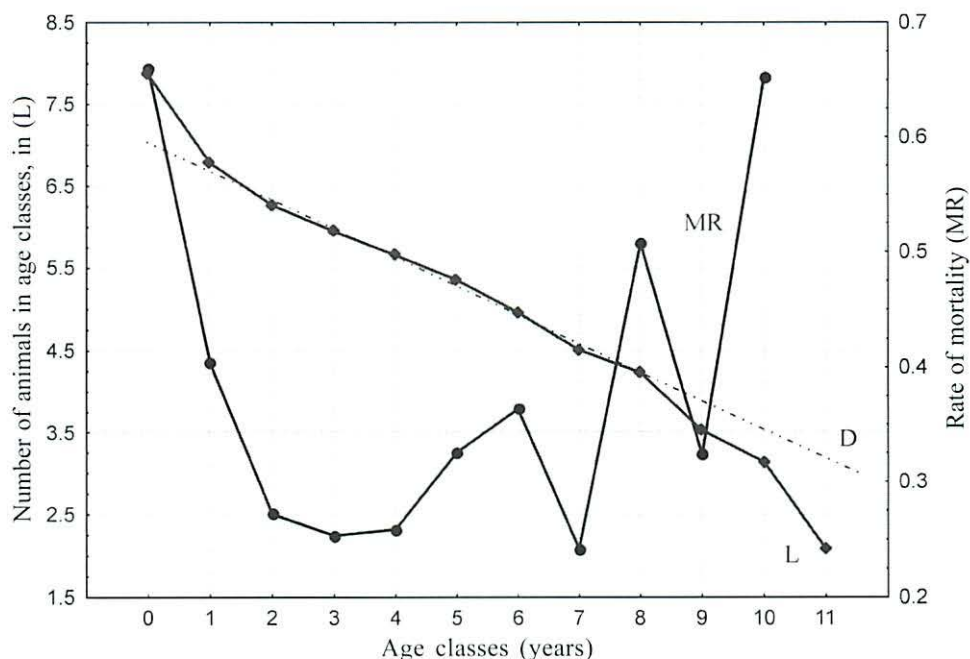


Fig. 5 Age distribution of the sable populations in western Sayan in 1963 – 1970 and 1977 – 1982. Line D shows the distribution recounted with the rate of mortality 0.286

The broad outline of the sable mortality, and its age changes, can be also seen by comparing figures on the survival of each age group for a one-year period (Fig. 5). After determining the percentage of survival by comparing the number of animals of some definite age in a selected group and the number of animals in the preceding age group, we can calculate mortality as an alternative index (Tab. 4).

The lowest mortality is registered amongst animals of 2 – 7 years old and has limits 0.242 – (M 0.286) – 0.364 (Tab. 4). It is also proved by data from the northern Sub-Urals 0.206 – (M 0.227) – 0.241; Tab. 1) and south-west Siberia ($M_5 = 0.354$ and $M_6 = 0.413$, according to the data of KRYUCHKOV 1974 and $M_7 = 0.260$ by data of LUKASHOV 1980 in Tab. 3).

By the graphical scheme of the age structure of the samples we can determine the presence or absence the raised mortality of young and old animals. If, in the scheme (Fig. 5) we assume the age distribution of classes 2 – 7 to be a straight line, and use it as a »plateau« (line D) according to SMIRNOV (1983), we can interpret the »burst« in the quota of young animals above line D as being selective hunting. Reduction in the senex portion can be explained by the fact that the animals of this group are the most difficult to catch. Besides this, their number is very small because of their high natural mortality.

Tab. 4 Age distribution, survival and mortality rates in sables of western Sayan in 1963 – 1970 (SOKOLOV 1979) and 1977 – 1982 (own data)

Age class	N (per mille)	Survival rate (SR)	Mortality rate	Distribution for SR = 0.714 (per mille)
0	492	0.340	0.660	291
1	167	0.596	0.404	208
2	100	0.728	0.272	148
3	73	0.747	0.253	106
4	54	0.741	0.259	76
5	40	0.675	0.325	54
6	27	0.636	0.364	39
7	17	0.758	0.242	28
8	13	0.493	0.507	20
9	6	0.677	0.323	14
10	4	0.348	0.652	10
11	2	–	–	7
12 – 14	4	–	–	–

If we assume that the rate of decrease for all age groups is the same for animals of 2 – 7 years old, then the number of juveniles in these tests should be 291 ‰ but not 492 ‰, as shown in Tab. 4. Correspondingly, the number of year-old animals should be 208 but not 167 ‰. The same method allowed also determination of the presumed age structure of the game samples from the northern Sub-Urals (Tab. 1, n”).

Studies on the population age structure in the basin of the Kizir River showed its significant difference ($t_d = 30.4$, $P < 0.001$) from that of the population of the central part of the western Sayan (for example, see Fig. 2). This became especially clear when we compared (Fig. 4) average ages: the River Kizir basin population is much younger ($t_d = 15.7$, $P < 0.001$) and has a less complicated structure. The reason for that is probably to be found in the different levels of hunting pressure. Hunting in the Kizir area is undertaken by skilful and clever hunters. This is the factor that determines the high reproductive performance and specific age structure of the Kizir population. In areas influenced by intensive hunting, animals of every group are caught at relatively higher intensities, and as the stronger is the pressure of hunting »the more general is the elimination« (SCHWARZ 1969). Consequently, rates of change of generations are higher, the structure of the population is less complicated, and the quota of young animals is higher. Such conclusion matches the results obtained by NUMEROV (1973). Probably, the influence of hunting on sable populations in the south-east of western Siberia (KRYUCHKOV 1974) is less important.

In the populations that are less affected by hunting, high fluctuations in numbers were found not only among juveniles but also for older age groups (> 1 and > 2 years) of sables. Under such conditions, female barrenness grows and their fertility reduces; the period of actual sexual maturation of young animals becomes longer, and mortality of young animals reaches its peak. As a result, the annual increment becomes lower (TIMOFFEEV & NADEEV 1955, ZALEKER 1962, POLUZADOV 1965, KHLEBNIKOV 1977). A greater number of age classes is typical for populations that are less exploited and less variable in their size, for example, in reserves.

Reproductive performance

Sable juveniles (age class 0) do not take part in the reproduction, therefore mating period takes place in July – August (when they are only 2 – 3 months old). Young animals, yearlings of age class 1 (to be more exact, aged 14 – 15 months old) do not always reach their sexual maturity and thus do not fully realise their reproductive potential (MANTEIFEL 1934, RAYEWSKY 1947, ZALEKER 1950).

We revealed the fertility of sable females by corpora lutea counts on histological preparations of ovaries (ZALEKER 1950). That procedure is an obligatory component of population monitoring in regional sable harvest management (e.g. ZALEKER 1956, VERSHININ 1963, MONAKHOV 1968). For example, in the northern Sub-Urals in 1978 – 1990, amongst animals in their 2nd year, the portion of pregnant females is 76.4 %, with 2.96 corpora lutea per each one and in the Kizir population 23.4 % and 0.64, accordingly. The same indices among all females older than 2 years of age were accordingly 94.2 % and 4.06 (in the Kizir population: 56.6 % and 1.92). The same results were obtained in other wild sable populations (BELOV 1980, KARTASHOV 1989) and in those from fur farms (MAMATKINA & MONAKHOV 1970, PAVLYUCHENKO et al. 1979). Usually sables fully realise their reproductive potential at an age of more than 2 years (MONAKHOV & BAKEEV 1981).

Reproductive Core

The reproductive core is defined as a group of animals, which is able to realise the maximum of their reproductive potential and thus constitutes the most stable part of a population (MONAKHOV 2001). Distinguishing the reproductive core is important because the animals belonging to this group are responsible for the population viability, especially under unfavourable and extreme conditions. The similar structural unit in a population, i.e. »a group of animals of both genders and of different age which determine the level of a reproductive cycle«, was defined by SOKOLOV (1979). However, the term »reproductive cycle« was not clearly defined by him.

The problem of distinguishing the reproductive core is closely connected with the accurate determination of population age structure because animals of different ages play quite different roles in reproduction (SCHWARZ 1959, 1969, YURGENSON 1966). This fact was proved by researches on both wild animals and those from fur farms (BAJEVSKY 1956, ZALEKER 1956, 1962, MONAKHOV 1968, 1971, 1973, MAMATKINA & MONAKHOV 1970). As already noted, sables can breed at the age of over 1 year old. However, the role of young animals in reproduction is limited for various reasons, i.e. their insignificant participation in reproduction, barrenness of females, and their low fertility. Higher intensity

of reproduction is characteristic for sables of 2 and more years old. The most fertile ones are females averaging 2 – 8 years old and sometimes older. It is considered to be normal that the age of females is directly proportional to embryonic or post-embryonic mortality of kits (SCHWARZ 1959).

In populations of wild sables, the share of animals of 8 years or older is 0.6 – 6.2 % (Tab. 3). Such a low proportion combined with high barrenness under usual conditions do not allow them to take part in the reproductive core with animals of 2 – 7 years old (MONAKHOV 2004a).

The highest rates of mortality were found among juveniles and senex animals (MONAKHOV 1983). Sables of different age are different in their receptiveness to diseases and helminth infections. After analysing a large dataset ($n = 1133$), it was found that the extensity and intensity of filaroidoses (nematode *Filaroides martis*) among young animals was higher than among adult ones (MONAKHOV 1999, 2001). Therefore, the reproductive core in sable populations should be considered as a group of animals of 2 – 7 years old.

Our research showed that quantitative changes in the reproductive core are of significantly less amplitude ($SD = 12.4\%$) as compared to animals of other age groups. Thus, as the role of this group within the population is very important, the result cannot be just accidental. The average shares of animals constituting the reproductive core are: 9.8 % in the northern Sub-Urals, 16.1 % in the basin of the River Kizir, and 38.0 % in the central part of western Sayan (according to SOKOLOV 1979). Fluctuations in this proportion closely correlated ($r = 0.86 - 0.91$) with variations in the average age M_a of a population (Fig. 4, Tab. 1, 2).

The highest results in reproduction are achieved by the young reproductive core. This fact was also noted by SOKOLOV (1979). The possible reasons for this may be amongst the following: either participation of relatively small numbers of females of older ages (5 – 7 years-old) in reproduction is limited, or after the core rejuvenation females of other ages (8 and older) take part in reproduction; or the fecundity of 5 – 7-year-old females is not sufficiently high (SOKOLOV 1979). The second reason seems to be the most probable because the average fertility of sable females correlates with their age ($r = 0.89$, $F = 3.22$, $P = 0.002$; MONAKHOV 1998).

Rejuvenation of the reproductive core in the course of population growth can be explained by incoming of young animals after seasons of favourable breeding in previous 2 – 3 years. This is a probable reason for 4-year periodicity in the number fluctuations of animals registered in many regions of sable area (POLUZADOV 1965, MONAKHOV & BAKEEV 1981, SAFRONOV & ANIKIN 2000). Changes in fertility, together with differential mortality, and variability in a number of breeding animals, allow the population to keep its number »on the level, adaptive to conditions of environment« (SHILOV 2001).

Thus, populations of sables consist of the following functional macrogroups: juveniles (sub-yearlings); year-old animals; animals forming the reproductive core (2 – 7 years old), and senex. The existence of the reproductive core is evident. In sable populations, the regulation is carried out on the basis of interaction between animals of different functional groups.

Finally, the data listed and their analysis allows us to make the following conclusions.

Dynamics of the size of sable populations mostly depend on fluctuations in the stock of juveniles. The highest level of mortality is registered amongst juveniles and senex, and the lowest one amongst the animals of 2 – 7 years old. The mortality rate of young animals depends on population structure and is adaptive to population density dynamics.

Population structure in regions with high hunting pressure is less complicated, the quota of young animals is relatively high, survival is lower; reproduction is higher, size fluctuations are stronger.

The reproductive core in wild sable populations consists of animals of 2 – 7 years of age. The increase in the share of animals drawing a reproductive core is accompanied by the decrease in the size of a population and its general growing-old. The young reproductive core is combined with high rates of increase, and vice versa.

Precise analysis of age structure gives an impression on mortality in different age groups in the population. Average age (M_a) can be used as an estimate of the dynamics in the population age structure, in its size, and also its rate of increase.

Control over age structure allows us to work out the correct way of exploiting sable populations (forecasting of harvest and hunting quotas).

5. Acknowledgements

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