

Size Structure of the Sable in the Lake Baikal Region: A Decadal Analysis over the Last Sixty Years

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Abstract—The skull sizes of eight Lake Baikal sable populations ($n = 1859$) were studied. It was noted that six of them constitute a homogeneous group of the small forms of the species. The decadal dynamics of 17 craniometric characters was analyzed. An increase in the skull size in the second half of the 20th century, common for both males and females, was revealed. The average growth trend over a decade was determined for the condylobasal skull length; it amounted to 0.15 mm in males and 0.11 mm in females. It was established that decadal deviations in sizes are, in most cases, not significant statistically; they are of an oppositely directed nature and do not disturb the species stability.

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INTRODUCTION

The influence of sizes on both the structure and functioning of an organism is considered to be quite significant (“the structure of an animal body, its most important systems and organs... is determined by its size”) (Kokshaiskii, 1987). Changes in sizes of animals have been known for a long time. Thus, directed changes in the sizes of animals of different species, which occur over large periods of time, were revealed and shown by Kurten (1959), Paaver (1964), Strel'nikov (1964), Raup and Stanley (1972) and others for many species, both fossil and modern. Decrease in size is found much more rarely (Kurten, 1959; Walvius, 1961; Smirnov, 1974).

The existence of such changes has allowed researchers to attribute them to a particular form of intraspecific variability in animals called the centenary variability (Paaver, 1964, 1965; Smirnov, 1977). It consists in changes that occur in the course of several dozen (hundreds) years. According to Paaver (1965, p. 80), “... it is characterized by an insignificant amplitude, reversibility, and rapidity of changes of distinct characteristics... .” He also notes that the centenary variability “... does not create any taxonomic differences yet but gives material for evolutionary transformations.” Until now, the centenary variability has been little studied and has not been given any sufficiently clear explanation.

Another pattern has also been described in the literature, known as the rule of phylogenetic growth of Cope–Depéret (Depéret, 1915; Shmalhausen, 1946; Rensh, 1960, and others) discovered by the American paleontologist Cope (1896). This pattern consists in a tendency to an increase in the size of animals in the

course of phylogenesis. Such an increase in sizes is characteristic of the sable as well (Monakhov, 1995, 2006).

The seasonal variability in the size of animals called the Dehnel phenomenon (Dehnel, 1949; Puzek, 1963; Mezhzherin, 1964, and others) is characteristic of species with the r-strategy of population dynamics but was also revealed for a number of long-living mammals, such as the Arctic fox, red fox, and stoat, but has not been found in the sable (Monakhov et al., 1988).

When conducting mass translocations of game animals in the middle of the 20th century with the formation of new beaver, raccoon dog, and sable populations, problems arose in the intraspecific taxonomy, as animals of other morphological forms (particularly, size) and subspecies, which were studied by many researchers, were released into the places of introductions (Shaposhnikov, 1958, 1963; Chashchin, 1960; Pawlinin and Shvarts, 1961; Kotov, 1967; Fedotov, 1967; Monakhov G.I. et al., 1982; Monakhov, 1995, 2006; Savel'ev, 2003; Korablev, 2005, and others).

The sable *Martes zibellina* L. is a valuable commercial fur species, which, in recent years, has constituted the basis of fur export of the country. According to the estimates of participants of the round table at the scientific research and practice conference devoted to the 90th anniversary of the All-Russian Research Institute of Hunting and Fur-Farming (Kirov, Russian Federation), the official auction sales reach 550 000–580 000 pelts at the end of the 2010–2011 season. Taking into account the volumes of the action of the internal market, the withdrawal from the populations was assessed to be 700 000 specimens. But even in the con-

ditions of the growing exploitation, the rational use of resources of the species is one of the main tasks of the Russian hunting sector of economy.

The sable from the Lake Baikal region is one of the most valuable race in the species areal in terms of its fur properties, a real gem of the Siberian taiga. By the 1940s, the areal of the sable consisted of several foci of residual habitation (Timofeev and Nadeev, 1955). When protective measures were taken, the population numbers started to recover, mainly through the reproduction and stabilization of the existing foci and subsequent colonization of the areas suitable for habitation. Artificial resettlement of animals had little significance in this process (Monakhov G.I. and Bakeev, 1981).

The following common names have long been used in the fur trade when characterizing the main “sable” region: the Baikal sable, Barguzin ridge sable, Cis-Baikal sable, etc., i.e., the animals that live in the environs of Lake Baikal, mainly in the taiga lands of the Irkutsk oblast, Republic of Buryatiya, and Zabaikal'skii krai, over a territory of ~1.03 mln km². However, a complete morphological characterization of the Trans-Baikal sables still does not exist. Some data are found only in the review of the geographical variability of the species in several monographs (Timofeev and Nadeev, 1955; Monakhov G.I. and Bakeev, 1981; Chernikin, 2006).

Craniological parameters are a widely used, relatively stable population characteristic, but the processes of growth and formation of the skeleton can be influenced by environmental conditions, such as the foraging base, temperature, etc. Skull size is one of the main taxonomic characteristics used in describing the intraspecies variability, including that of the sable. Many zoologists used skull sizes—the main and condylobasal skull lengths, zygomatic width, largest width and height, etc.—as subspecies parameters (as a rule, taking into account the sex of the animals). Ognev (1925, 1931) was the first who use craniometry in describing subspecific sable forms. Afterward, skull measurements were actively used for identifying the species and reviewing the taxonomy of the sable (Kuznetsov, 1941; Timofeev and Nadeev, 1955; Geptner et al., 1967; Monakhov G.I., 1976; Pavlinov and Rosolimo, 1979). Some authors (Kazarinov, 1954; Pavlinin, 1966; Tavrovskii, 1971; Monakhov G.I. and Bakeev, 1981; Monakhov, 2006) use the data of craniometry for general or local reports, while others (Ramenskii and Monakhov, 1984; Monakhov, 1988, 2006; Monakhov et al., 1988) use them to reveal directed changes in sizes with time and studying the sexual dimorphism (Monakhov, 2009, 2012). The sizes of the sable are considered to be the main taxonomic characteristics (Monakhov, 2011), which are also significant in fur merchandizing.

The aim of this work is to analyze long-term decadal data on the sizes of the Baikal sable using metric parameters of the skull.

MATERIALS AND METHODS

Skull sizes were analyzed for eight Baikal populations of the species: from the mountain systems of Barguzin, East Sayan, Khamar-Daban, lower basin of the Vitim River, upper reaches of the Nizhnyaya Tunguska, Lena, and Chikoi rivers, and the middle basin of the Angara River (Table 1) (Monakhov G.I., 1976). Samplings from the collections of the Zoological Museum of the Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences (Yekaterinburg), the Zoological Museum of Moscow State University (Moscow), the East Siberian Branch of the All-Russia Research Institute for Hunting and Fur-Farming (Irkutsk), Baikal Nature Reserve (Tankhoi village, Republic of Buryatiya), and private collections of Yu.M. Baranovskii (Irkutsk) and G.M. Agafonov (Menza village, Zabaikal'skii krai).

To compare with the Baikal populations, in order to demonstrate the geographical differences in size, we used a lot of groupings from other parts of the specific areal (Table 1). The most contrasting of them were selected in order to estimate the degree of similarity and difference of sables by this trait. The skulls of adult animals older than one year old were measured using sliding calipers (with an accuracy of up to 0.1 mm) by 17 standard metric parameters of the skull. The age was determined according to the methods of Timofeev and Nadeev (1955) and Smirnov (1960). The size ratios of the samplings were evaluated using the method of the main components, cluster and regression analyses (Statistica 6). The following statistical parameters were used: (*p*) the level of significance, (*r*) correlation coefficient, (*R*²) determination coefficient; and (*F*) Fisher's test (the underline indices indicate the numbers of the degrees of freedom) and the average values for the samplings.

RESULTS AND DISCUSSION

In all studied population groups, according to the averaged values of the parameters, the condylobasal lengths (CBL) of the male and female skulls constitute 80.17–83.14 and 73.48–75.93 mm, respectively. In the craniometric structure of the species, six Baikal groups belong to the cluster of small skulls and only two groups (middle Angara and Low Tunguska) are in the “middle” cluster (Fig. 1) (Monakhov, 2006). For comparison, the maximum sizes in the areal were characteristic of the Kamchatka sables (males 87.9 and females 81.0 mm) and the sables of Southwest Altai (88.3 and 80.6 mm, respectively), which composed the cluster of the largest skulls. The “large” cluster includes the western populations of the Mid Urals and Ob' River region, whose CBL is 85–86 mm in males and 78–79 mm in females (Fig. 1).

As an integral indicator of the sizes (measured in the Euclidean distance (ED)), we used the first principal component (PC1 score, Table 2, and Fig. 2). 1PC

Table 1. Studied material and characteristics of the localities

Localization (designation)	Geographical coordinates, degrees (N/E)	Years (number of decades)	Studied material		
			males	females	total
East Sayan Ridge (VS)	53/100	1960–1990 (3)	125	119	244
Khamar-Daban Ridge (HD)	51/105	1960–2000 (3)	153	132	285
Upper reaches of the Chikoi River (CH)	50/110	1960–1990 (2)	90	82	172
Middle Angara (AN)	56/101	1960–1990 (3)	91	102	193
Upper reaches of the Lena River (LE)	56/107	1960–1990 (3)	143	146	289
Upper reaches of the Lower Tunguska River (NT)	61/108	1960–1990 (2)	42	38	80
Barguzin ridge (BA)	55/110	1950–1990 (5)	152	157	309
Lower reaches of the Vitim River (VT)	58/113	1960–1990 (4)	154	133	287
Total		1950–2000 (6)	950	909	1859
Groups from other parts of the areal					
Upper reaches of the Loz'va River (LOZ)	61/61	1931–1989	56	48	104
Tapsui, North Sos'va rivers (TAP)	64/61	1937–1958	52	52	104
Pelym River (PEL)	61/62	1951–1980	38	23	61
Southwest Altai (SWA)	50/84	1954–1972	94	81	175
Sikhote-Alin' Ridge (SIH)	47/138	1969–1989	201	161	362
Kamchatka Peninsula (KAM)	56/159	1929–1996	196	190	386
Total			637	555	1192

covers 95.9% of the explained dispersion of the skull sizes, so its value can be used as an integral indicator in estimations and comparisons. The connection of such widely used parameters as the CBL with the 1PC score proved to be similar and highly significant for both males ($r = 0.97$, $p < 0.0001$, and $F_{1,23} = 324.2$) and females ($r = 0.96$, $p < 0.0001$, and $F_{1,23} = 293.2$).

Classification of the studied samplings using the method of clusterization by the averaged data divides them into two groups: large and small (Fig. 3). The samplings from the Angara and Low Tunguska rivers belong to the conditionally large: CBL of males and females is >82 and >75 mm, respectively. 1PC in males is >1.3 ED and in females >-0.7 ED.

The relation between the skull sizes and the geographical location of the area of habitation of the groups was studied. No connection with the longitude was revealed. The connection with the latitude of the area by CBL was positive and statistically significant: in males $r = 0.61$ ($p = 0.0012$ and $F = 13.6$) and in females $r = 0.68$ ($p = 0.0002$, $F = 20.1$), which indicates an increase in the skull sizes from the south to the north and correspondence with Bergman's well-known ecogeographical rule.

The material allowed us to perform chronological comparisons of the size parameters of the populations with decomposition into subsamplings belonging to different decades of the second half of the 20th century. Twenty-five such samplings were counted (Table 2).

Analysis of the obtained values of the characteristics (Table 2) allows us to estimate the dynamics of the parameters by decades. At the same time, the values of the decadal deviations of CBL are, as a rule (61.8% of cases), statistically insignificant ($p > 0.05$). But in the

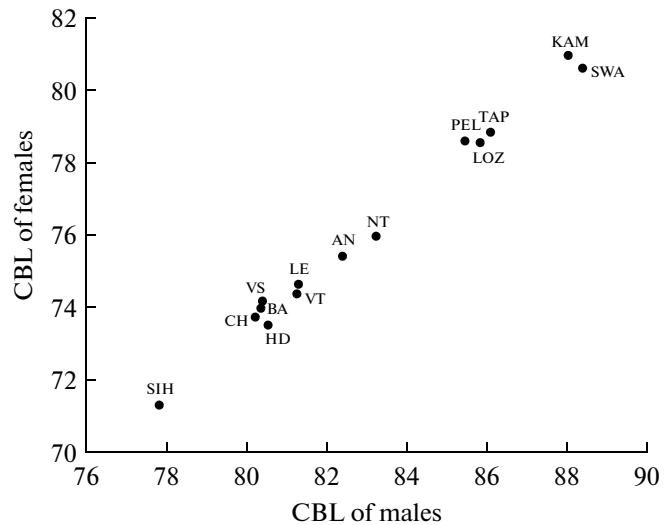


Fig. 1. Position of the Baikal populations in the species craniometric structure of the sable (Table 1). CBL are condylobasal lengths; for Figs. 1 and 2.

Table 2. Characterization of the skull sizes of sables in the studied populations of the Lake Baikal region (mm, mean values for the samplings)

Decadal samplings	$n \text{ ♂/♀}$	CBL		Length of the teeth row		PC1 score	
		males	females	males	females	PC1M	PC1F
East Sayan Ridge 1960 (VS60)	74/55	79.67	73.75	31.1	28.47	-1.1	-0.65
1980 (VS80)	27/37	82.27	74.92	31.36	28.2	0.91	0.30
1990 (VS90)	24/27	80.23	73.97	30.86	28.21	-0.74	-0.36
Khamar-Daban Ridge 1960 (HD60)	62/45	80.12	73.27	30.85	27.74	-0.76	-1.22
1990 (HD90)	55/45	80.33	73.48	30.73	27.66	-0.7	-1.28
2000 (HD00)	36/42	81.32	73.7	31.11	27.89	0.28	-0.51
Chikoi River 1960 (CH60)	59/54	80.43	73.59	30.64	27.83	-1.33	-1.49
1990 (Ch90)	31/28	79.67	74.07	30.48	27.99	-1.57	-0.98
Angara River 1960 (AN60)	53/51	82.04	75.35	31.57	28.79	1.04	0.87
1980 (AN80)	21/23	82.5	75.25	31.75	28.65	1.36	1.06
1990 (AN90)	17/28	82.99	75.59	32.10	28.55	1.55	1.35
Lena River 1960 (LE60)	54/53	80.44	73.88	31.55	28.15	-0.26	-0.34
1980 (LE80)	58/58	81.62	75.03	31.34	28.49	0.57	0.70
1990 (LE90)	31/35	81.86	75.04	31.44	28.59	0.64	0.81
Upper reaches of the Lower Tunguska River 1960 (NT60)	22/20	82.5	75.5	31.44	29.1	1.11	1.57
1990 (NT90)	20/18	83.85	76.41	31.93	29.09	2.05	2.46
Barguzin Ridge 1950 (Bg50)	21/19	81.81	74.89	31.38	28.55	0.77	0.81
1960 (Bg60)	55/55	79.55	74.05	30.42	28.16	-1.44	-0.60
1970 (Bg70)	12/16	81.14	74.19	30.76	28.20	-0.43	-0.23
1980 (Bg80)	39/37	80.35	73.61	31.07	28.28	-0.5	-0.75
1990 (Bg90)	25/30	80.18	73.65	31.02	27.93	-0.67	-0.95
Vitim River 1960 (Vt60)	58/48	80.62	74.32	31.07	27.61	-0.79	-0.79
1970 (Vt70)	32/28	81.68	74.25	31.31	28.23	0.18	-0.10
1980 (Vt80)	48/43	81.68	74.28	31.42	28.53	0.27	-0.04
1990 (Vt90)	16/14	81.05	74.71	31.13	28.29	-0.43	0.36

majority of cases of significant differences, the trends are of the oppositely directed vectors.

The correspondence of the decadal changes in the skull sizes in males and females is the highest (88.2% cases): 1PC: $r = 0.83$ ($p < 0.0001$, $R^2 = 0.70$; and $F_{1,15} = 34.5$). Variation of sizes of 1PC (ED, minimum/mean/maximum) is as follows: 0.65/0.043/0.62 in males and 0.31/0.056/0.25 in females. On the whole, tendencies of growth in sizes prevail (the mean values are positive), which is confirmed graphically in Fig. 2. Although the variation range into both direction is 2–3 times higher in males, the mean deviation in females is higher by 30% than in males (0.053 and 0.046 ED, respectively).

The trends of increase are registered, for example, for the CBL: the variation range of this character in males is 2.2–2.4 times higher than in females. The variation of CBL in males is -2.3...+2.6 and -1.0...+1.2 mm in females with average values of 0.21 and 0.15 mm, respectively ($p > 0.05$). The correspondence of the dynamics of CBL between the sexes is also sufficiently high, 71%.

Earlier, the chronographical variability of the skull sizes of the sable was studied by us (Monakhov, 2006) for two Baikal populations (from Barguzin Ridge, for 1950–1980 (four decades) and from the basin of the Vitim River for 1960–1980 (three decades)), as well as by Ranyuk and Sutula (2008) for the Khamar–Daban ridge populations for 1960–2000s who used the craniometric data presented by us. It was shown in these

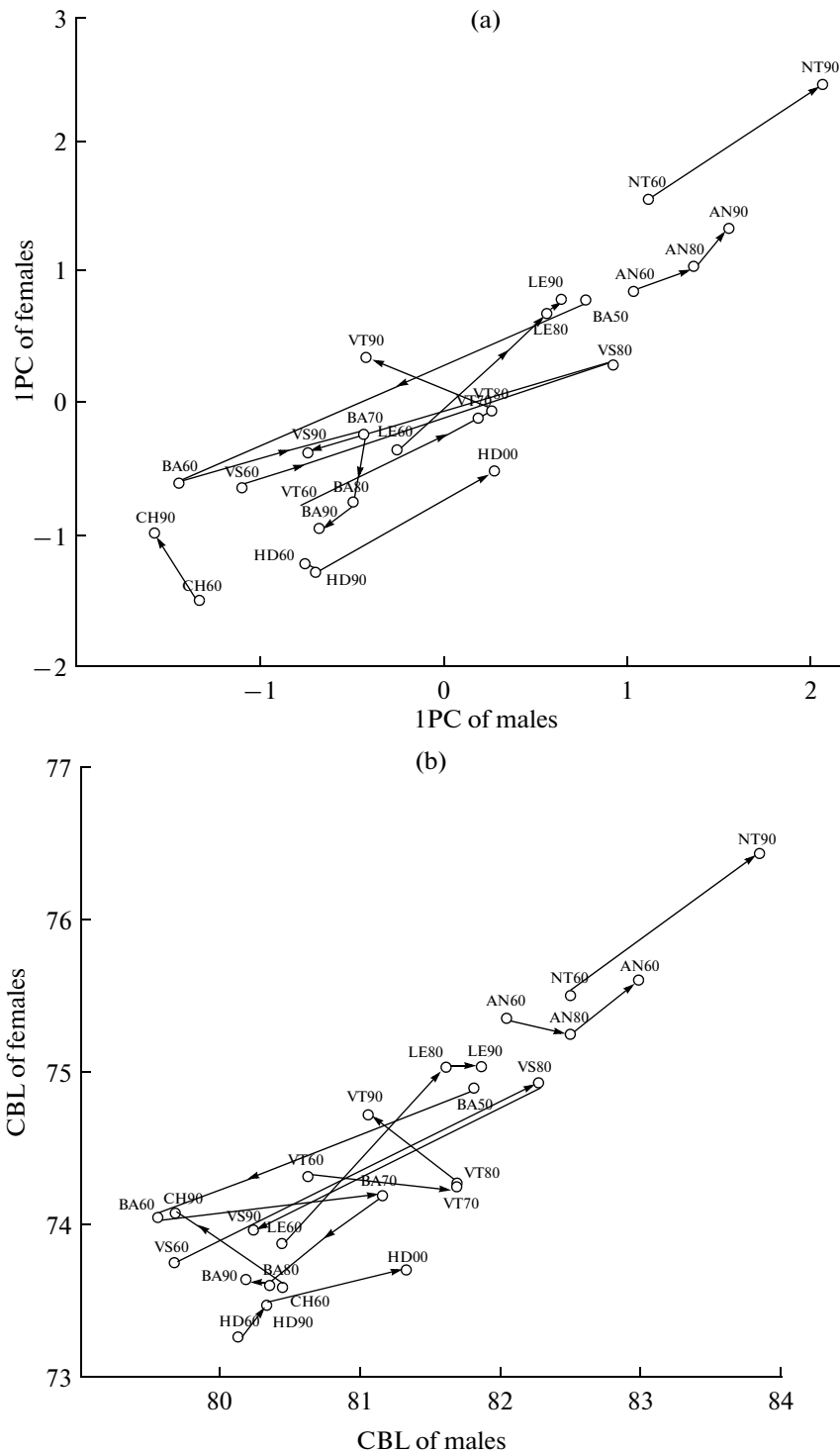


Fig. 2. Geographical trajectories of the craniometric chronotrends of the Baikal sable regarding (a) IPC and (b) CBL of the skull. The designations of the samplings are given in Table 2.

publications that the dynamics of the skull sizes manifests itself not only in the three Baikal populations but is also characteristic of the populations from other parts of the areal of the species (Ural region and mid-Siberia).

On the whole, in the second half of the 20th century, the sables in the Baikal region increased in size (both males and females), which was registered for six populations; the sables from Barguzin Ridge were characterized by a general decrease; while in the basin

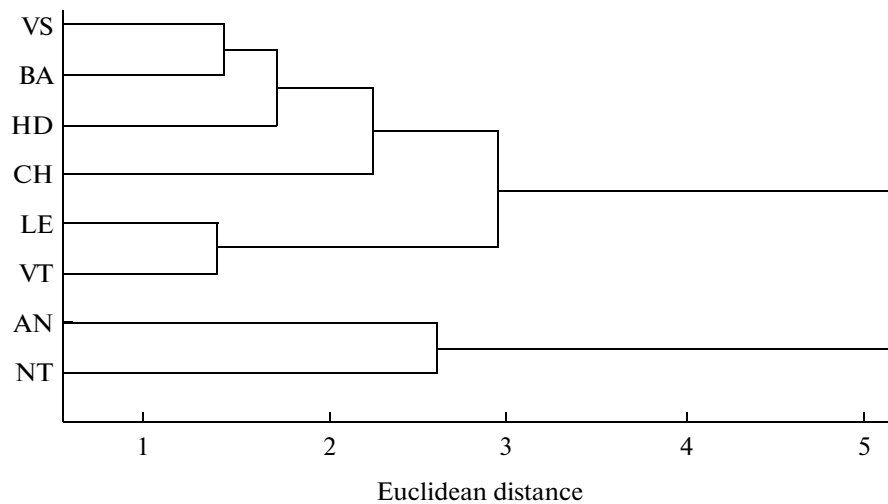


Fig. 3. A dendrogram of the cluster analysis of the Baikal sable populations by the skull sizes.

of the Chikoi River, the increase of females was accompanied by the decrease of males. In most cases (more than two decades), the changes were nonlinear and of reciprocal nature, which indicates the tendencies to stability of the morphological appearance of the populations and specific characteristics of the sable.

At the same time, the tendencies to increase in size evidence the normal development of populations in agreement with the well-known Cope–Depéret rule of phylogenetic growth, according to which a tendency to increase in the size of the body of organisms is observed in each phylogenetic line, i.e., the development goes from small ancestor groups to larger ones. This is often accompanied by the settlement of the species (species expansion, radiation).

For each group, a decadal trend was calculated, i.e., the rate of change of sizes over one decade. For instance, in the metrics of IPC, the average trend over a decade was (ED; minimum/mean/maximum) $-0.10/0.03/0.10$ for males and $-0.11/0.04/0.10$ for females, while CBL was $-0.41/0.15/0.47$ and $-0.31/0.11/0.39$ mm, respectively. Therefore, the calculations confirmed the revealed tendency of growth of sizes, which is more pronounced in males.

Thus, out of the eight studied Baikal sable population groups, six belong to small populations (CBL 79.6–82.3 mm in males and 73.3–75.3 mm in females) and constitute a rather homogeneous group of populations, while the two populations that inhabit the northwest of the region (Angara and Lower Tunguska) are considered average (CBL 82.0–83.9 mm in males and 75.0–76.4 mm in females (Fig. 2)). The differences between the macrogroups by the median test are statistically significant ($p < 0.05$) for both males and females.

Let us recall that minimum sizes are registered on Sikhote-Alin' Ridge and in the lower Amur River

region, from where the clinal increase in the sizes of sables (Monakhov G.I., 1976; Monakhov, 2006) in the western and northwestern directions takes place. We believe this effect a consequence of the species expansion throughout Siberia from the southeastern regions of the refugial concentration of the sable in the period of the Sartan glacial maximum.

One of the possible factors of trends could be the long-term change in the climate of the region. Restoration of the sable abundance in the Baikal region occurred against the background of a considerable warming of the climate (Kovalenko and Yudina, 1999; *Doklad ob osobennostyakh klimata ...*, 2009). According to the data of Gruza and Ran'kova (2003), the trend of change in the average annual air temperature ($3.5^{\circ}\text{C}/100$ years) was the most intensive over all of Russia in 1951–2000. In the same period, according to our data (Monakhov, 2007), an intensification of the reproductive cycle in sable populations occurred in the Ural region.

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